A highly diverse bivalve fauna from a Bithynian (Anisian, Middle Triassic) Tubiphytes -microbial buildup in North Dobrogea (Romania)

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A highly diverse bivalve fauna from a Bithynian (Anisian, Middle Triassic) *Tubiphytes*-microbial buildup in North Dobrogea (Romania)

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Abstract

This paper describes a rich bivalve fauna from the *Tubiphytes*-Limestone Member (Bithynian, early middle Anisian) of the Caerace Formation in North Dobrogea (Romania). We report 51 bivalve species, including seven new species and two new genera: *Atrina multicostata* n. sp., *Pinna simionescui* n. sp., *Chlamys* (*Praechlamys*) *prima* n. sp., *Entolium reticulatum* n. sp., *Scythentolium anisicum* n. sp., *Romaniamya mahmudiaensis* n. gen. et n. sp. and *Praedicerocardium vetulus* n. gen.

et n. sp. The latter taxon represents the oldest Triassic megalodontoid. We provide detailed descriptions of the bivalve fauna, discuss the ecology and compare species richness in the Early and Middle Triassic, showing that the bivalve assemblage of North Dobrogea is much more diverse than all previously described Early Triassic bivalve faunas, but not as rich as several faunas from the late Anisian and Ladinian. The relative richness of the Dobrogea fauna with respect to geologically older and younger faunas suggests that it represents an early stage of the main rediversification of bivalves after the end-Permian mass extinction.

Keywords: Bivalvia, Anisian, Bithynian, North Dobrogea, diversity, recovery.

The most severe biotic crisis in Earth's history, the end-Permian mass extinction about 252 Ma ago (Burgess *et al.* 2014), did not only extinguish between 81% (Stanley 2016) and 96% (Raup 1979) of all marine species, but also caused a temporal shift from the Upper Paleozoic T-type ('tropical') carbonate factory to a non-skeletal M-type ('mud-mound') carbonate factory (*sensu* Schlager 2000, 2003; Baud & Richoz 2004; Baud *et al.* 2007). While M-factory reefs already flourished during the Early Triassic (e.g. Brayard *et al.* 2011; Friesenbichler *et al.* 2018), T-factory reefs started re-diversifying since the Middle Triassic (Flügel & Stanley 1984; Stanley 1988; Senowbari-Daryan *et al.* 1993; Flügel 1994, 2002; Martindale *et al.* 2019). One of the last 'pure' M-type Triassic carbonate factories before the transition toward T-type factories is a *Tubiphytes*-microbial buildup located in the Mahmudia Quarry in the North Dobrogea Orogen (Popa *et al.* 2014), which is also one of the few bioconstructions from the Tethyan realm that flourished during the Bithynian (early middle Anisian, Middle Triassic).

The *in situ* boundstones of the *Tubiphytes*-microbial buildup developed on the upper slope of a distal platform in relatively deep water under normal oxic conditions and in an intertropical environment (Forel & Grădinaru 2018). It was built up by a micro-framework of *Tubiphytes*, a small encrusting and low-tiering organism of uncertain affinities (Riding & Guo 1992) that is a common fossil in Anisian reef assemblages. Apart from the micro-framework of *Tubiphytes*, the buildup contains abundant fine-grained internal sediments, microbial crusts and autochthonous micrite, added by a large volume of marine cements (Popa *et al.* 2014). The *Tubiphytes*-microbial buildup provided a suitable environment for various groups of abundant and diverse benthic macroinvertebrates such as bivalves, gastropods (Nützel *et al.* 2018) and brachiopods (Grădinaru & Gaetani 2019), plus a rich ostracod fauna (Forel & Grădinaru 2018).

The Bithynian *Tubiphytes*-microbial buildup is one of the oldest Triassic carbonate reefs and provides the opportunity to study how bivalves adapted to this new habitat type and how this affected their recovery after the end-Permian mass extinction. This study is part of a series of studies (Forel & Grădinaru 2018; Nützel *et al.* 2018; Grădinaru & Gaetani 2019) that aim at the systematic description and interpretation of the fossil content from the *Tubiphytes*-microbial buildup in North Dobrogea. We report 51 bivalve species belonging to 39 genera, which makes bivalves the most diverse macroinvertebrate group of the *Tubiphytes*-microbial buildup so far. Seven species and two genera are newly described, including the oldest Triassic representative of the Megalodontoida. The ecology of the bivalve fauna is reconstructed and its species richness is discussed in the context of the rediversification of marine life after the end-Permian mass extinction.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The North Dobrogea Orogen is located in the foreland of the Alpine Carpathian Orogen (e.g. Săndulescu 1995) and is limited by the Danube Delta in the North and the Black Sea in the East. It is the westernmost segment of the Palaeo-Tethyan Cimmeride Orogenic System and continues eastward into the Mountainous Crimea, the North Caucasus (Fig. 1A, inset map) and further eastwards into the Asian Cimmerides (Săndulescu 1980; Şengör 1984, 1986). The North Dobrogea Orogen is a fold-and-thrust belt that consists of several tectonic units (Fig. 1A. Visarion *et al.* 1990; Săndulescu 1995). The Triassic succession has its widest extent In the Tulcea Unit, which is the lowermost tectonic unit of the North Dobrogea Orogen and is located in its eastern part. The Triassic sediments unconformably overlie the Variscan basement and are developed both in basinal and carbonate platform facies (Grădinaru 1995, 2000). During the Middle Triassic, a carbonate platform developed in the central and eastern areas of the Tulcea Unit. The various carbonate facies that developed in the eastern area of the Tulcea Unit are described in detail by Popa *et al.* (2014). The North Dobrogea Orogen, with its Tethyan-type Triassic succession, is tectonically bounded by the Scythian Platform in the north and the Moesian Platform in the south (Fig. 1A), where the Triassic is of Germanic type (Grădinaru 1995, 2000). The remote location of the North Dobrogea Tethyan-type Triassic outside the Mediterranean Triassic is interpreted as a result of post-Triassic large-scale horizontal displacements of Tethyan terranes due to the opening of the West Black Sea Basin (e.g. Grădinaru 1988; Okay *et al.* 1994; Banks & Robinson 1997).

The studied material comes from the Mahmudia Quarry (45° 03‘ 12.41‘‘ N, 29° 03‘ 34.52‘‘ E), which is located in the Caeracul Mare Hill area, south of the village of Mahmudia, 35 km east of Tulcea (Fig. 1A–B). The Middle Triassic Caerace Formation that is exposed in this limestone quarry can be subdivided into the Stromatactis-Limestone Member and the *Tubiphytes*-Limestone Member (Fig. 1C and Fig. 2). The latter is exposed in the northeastern part of the quarry and represents a *Tubiphytes*-microbial buildup that was first documented by Dobre-Popa (2011) and Popa *et al.* (2014). It yields a rich macroinvertebrate fauna consisting of coiled nautiloids, ammonoids, bivalves, gastropods, brachiopods, sponges and crinoids (Popa *et al.* 2014; Forel & Grădinaru 2018; Nützel *et*

al. 2018; Grădinaru & Gaetani 2019). The ammonoids found in the *Tubiphytes*-Limestone Member can be correlated with the Bithynian (early Middle Triassic) *Osmani*-ammonoid Zone of the Northwestern Caucasus (Shevyrev 1995) and the lower part of the middle Anisian, i.e. the *Hyatti*-ammonoid Zone of northwestern Nevada (Silberling & Nichols 1982; Bucher 1992; Monnet & Bucher 2006). The *Tubiphytes*-microbial buildup is a massive carbonate buildup without well-expressed bedding and consists of several different carbonate facies (Popa *et al.* 2014). Among these are frequent packages of microbially mediated cement crusts, which were generated by syndepositional microbial mats. These microbial mats and their cement crusts provided taphonomic conditions that were favourable for the preservation of minute details of the ornamentation of fossil shells and the primary colour patterns of some gastropods (Popa *et al.* 2014; Forel & Grădinaru 2018; Nützel *et al.* 2018). So far, only few data has been published on Triassic bivalves from the North Dobrogea Orogen (Peters 1867; Kittl 1908; Simionescu 1908, 1910*a*, *b*, 1911, 1925; Mirăuță & Iordan 1982; Mirăuță *et al.* 1984), making the present work a significant contribution to the knowledge of the bivalve fauna from this Tethyan-type Triassic development.

MATERIAL AND METHODS

The bivalve fauna presented herein comes from one sample of *c.* 1.5 m^3 rock material from the *Tubiphytes*-Limestone Member (Fig. 1C–D and Fig. 2) that yielded several hundreds of macroinvertebrate fossils. For taxonomical identification, a total of 303 bivalve specimens were mechanically prepared from the rock with micro-jacks. The terms small, medium sized and large are used for specimens that are smaller than 2 cm, between 2 and 5 cm or larger than 5 cm, respectively. The 303 specimens represent a minimum of 214 individuals. This number was inferred from counting

the most numerous valves, left valves (LVs) or right valves (RVs), together with articulated specimens. The number of individuals was the basis for a rarefaction analysis (Sanders 1968), which was performed to assess the relative completeness of sampling and to compare the diversities of the present bivalve fauna with other Early and Middle Triassic bivalve assemblages. Ecological parameters like Simpson's index of dominance (Simpson 1949) and rarefaction analysis were calculated with PAST version 2.17 software (Hammer *et al.* 2001). For further taxonomical as well as ecological characterization of the bivalve fauna, rank-abundance distributions (Whittaker 1965) and pie charts were used. The modes of life were inferred from literature data, functional morphology and the mode of life of related Recent taxa. For photographing, specimens were covered with ammonium chloride. The comparison of diversities of Early and Middle Triassic bivalve faunas is based a previous analysis (Friesenbichler *et al.* 2019) and additional literature. The occurrences of identified bivalve species and genera during the Early and Middle Triassic was analysed based on the literature including the compendium of Ros-Franch *et al.* (2014). The bivalve samples are housed in the Collection of the Museum of the Laboratory of Palaeontology in the University of Bucharest.

SYSTEMATIC PALAEONTOLOGY

Our systematic arrangement is based on Cox *et al.* (1969), Hautmann (2001*a*) and Bieler *et al.* (2014), with additions from Allasinaz (1972), Waller & Stanley (2005), Hautmann (2008), Carter *et al.* (2011), Hautmann *et al.* (2013) and Hofmann *et al.* (2014).

Class BIVALVIA Linnaeus, 1758

Subclass PTERIOMORPHIA Beurlen, 1944

Order ARCOIDA Stoliczka, 1871 in Stoliczka 1870–1871

Superfamily ARCOIDEA de Lamarck, 1809

Family PARALLELODONTIDAE Dall, 1898

Genus PARALLELODON Meek & Worthen, 1866

Type species. *Macrodon rugosus* Buckman in Murchison *et al.,* 1845.

Parallelodon? sp.

Figures 3A–B

Material. One incompletely preserved LV.

Description. Shell medium sized, posteriorly elongated, moderately inflated; dorsal margin long and straight, posterior margin slightly concave, ventral margin convex; ligament duplivincular, posterior part of ligament area with subparallel grooves representing traces of duplivincular ligament system (Fig. 3B); carina rounded, extending to postero-ventral part of shell, bordering slightly impressed posterior area; irregular growth lamellae most clearly visible near shell margins.

Remarks. The shape, outline and duplivincular ligament area indicate that this specimen belongs to the Arcoida. Among Middle Triassic arcoids, three species are similar in terms of the elongated outline and the presence of an irregular concentric sculpture: *Parallelodon beyrichi* (von Strombeck, 1849), *P. esinensis* (Stoppani, 1858) and *P. impressum* (Münster, 1841). In *P. esinensis* this concentric sculpture is best visible at the shell margins. Furthermore, it possesses a rounded carina, which is also the case in the Dobrogea specimen. However, Posenato (2008) mentions a very shallow but wide sulcus in the middle part of the shell in front of the carina, which is not observable in the Dobrogea specimen because of its incomplete preservation. Apart from that, the antero-ventral margin of *P. esinensis* is more rounded compared to the antero-ventral margin of the Dobrogea specimen, which is more similar to the antero-ventral margin of *P. beyrichi*. However, like *P. esinensis*, *P. beyrichi* possesses a shallow median sulcus that runs from the beak to the ventral margin. Furthermore, radial ribs were reported on the area of *P. beyrichi*, a feature that is not observable in the Dobrogea specimen. As well as *P. beyrichi*, *P. impressum* possesses a sulcus and radial ribs. However, this sulcus is only present in juvenile specimens and the radial ribs are neither observable with naked eye nor are they present in all specimens of *P. impressa*. Already Salomon (1895, p. 163–165) pointed out that *P. impressum* and *P. beyrichi* cannot be clearly distinguished from each other; therefore he united both species as *P. impressum*. Furthermore, he proposed that *P. impressum* could possibly represent juvenile specimens of *P. esinensis*. Currently, the problem of possible synonymies cannot be resolved and an assignment of the Dobrogea specimen to any of these species is uncertain. Therefore we present it in open nomenclature and provisionally assign it to the genus *Parallelodon*.

Ecology. According to Stanley (1972), the genus *Parallelodon* comprises endobenthic as well as epibenthic species. Yin & McRoberts (2006) suggested that species of this genus had an epibyssate and suspensivorous mode of life.

Order MYTILIDA Férussac, 1822 in Férussac 1821–1822

Superfamily MYTILOIDEA Rafinesque, 1815

Family MYTILIDAE Rafinesque, 1815

Genus MODIOLUS de Lamarck, 1799

Type species. *Mytilus modiolus* Linnaeus, 1758.

Modiolus sp. A

Figures 3C–D

Material. Two incompletely preserved LVs.

Description. Shell medium sized, modioliform, retrocrescent, inequilateral; dorsal margin slightly convex, passing gradually into convex posterior margin, ventral margin concave; beak acute, prosogyrate, subterminal; byssal gape well developed (Fig. 3D), located at one third of antero-ventral margin; anterior shell lobus small; irregular growth lamellae, best visible at posterior and ventral margin.

Remarks. The shape, outline and the presence of a byssal gape are indicative for the genus *Modiolus*. Already Bittner (1901, p. 21) noted the difficulties in differentiating between species among Triassic

representatives of this morphologically variable genus. Because of its incomplete preservation, we present the Dobrogea specimens in open nomenclature.

Ecology. Endobyssate suspension-feeder (Stanley 1970, 1972).

Modiolus sp. B

Figure 3E

Material. One incompletely preserved LV.

Description. Shell small, modioliform, slightly inflated; beak acute, prosogyrate, subterminal; antero-ventral margin nearly straight, posterior margin curved; very fine and regular growth lines.

Remarks. This taxon differs from *Modiolus* sp. A in being less upright and having a straight antero-ventral margin and fine, regular growth lines.

Ecology. Same as for *Modiolus* sp. A.

Order PTERIOIDA Newell, 1965

Suborder PTERIINA Newell, 1965

Superfamily PINNOIDEA Leach, 1819

Family PINNIDAE Leach, 1819

Remarks: Three genera of Pinnidae have been reported from the Triassic: *Pinna* Linnaeus, 1758, *Atrina* Gray, 1842 and *Mesopinna* Vu Khuc & Huyen, 1984. One character used for the distinction of *Pinna* and *Atrina* is the shape of the nacreous region on the shell interior. The nacre in *Pinna* is medially devided into two lobes, whereas the nacreous region in *Atrina* is continuous (Cox *et al.* 1969). Another commonly used criterion for distinguishing *Pinna* and *Atrina* is the presence or absence of a medial carina. Accordingly, *Atrina* does not possess a medial carina, which is present in *Pinna*, at least in earlier growth stages (Cox *et al.* 1969; Waller & Stanley 2005; Koppka 2018). However, according to Hyatt (1892) and Turner & Rosewater (1958) both genera show little morphological difference with respect to the medial carina during their early ontogenetic stages. Therefore, the differentiation of both genera based on the presence or absence of a medial carina is only possible for adult specimens. Moreover, only few Triassic species assigned to *Pinna* demonstrably possess a medial carina (Waller & Stanley 2005; McRoberts 2017). This could mean either that these species do not belong to *Pinna*, or that the presence of a medial carina does not sufficiently diagnose this genus. Another character used to distinguish *Pinna* from *Atrina* is the shape. According to Cox *et al.* (1969) and Waller & Stanley (2005), *Atrina* is ham-shaped with a rounded posterior end, whereas *Pinna* is wedge- to ham-shaped. *Mesopinna*, the third Triassic pinniid genus, was described by Vu Khuc (1991) as pinniform (i.e. wedge-shaped), with a weakly pronounced medial carina, a lenticular shell cross section at the umbonal region and a concentric sculpture.

The material described below demonstrates the difficulty of a consistent separation of *Pinna* and *Atrina* based solely on one criterion. Since the nacreous regions of the shell's interior are not

observable, we cannot use this criterion for the differention between *Pinna* and *Atrina*, but we found that a more pronounced carina correlates with a more wedge-shaped outline, whereas a short carina corresponds to a ham-shaped overall morphology. We therefore suggest tentatively that *Pinna* is wedge-shaped to slightly ham-shaped and has a medial carina that was present during most of its ontogeny, whereas *Atrina* is clearly ham-shaped, with a medial carina either absent or present only during its earliest ontogeny. The main difference between *Pinna* and *Mesopinna* is the absence of radial ribs in *Mesopinna*, which, in our opinion, is insufficient to justify its separation from *Pinna*.

Genus ATRINA Gray, 1842

Type species. *Pinna nigra* Dillwyn, 1817.

Atrina multicostata n. sp.

Figure 3H

LSID. urn:lsid:zoobank.org:act:41925AAC-F737-41D4-8631-2AB10A18BCF7

Derivation of name. Combination of *multi* (Latin: many) and *costata* (Latin: ribbed).

Holotype. LPB IIIL 2005

Material. One LV.

Diagnosis. *Atrina* with at least 40 radial ribs with rounded crests that get broader towards posterior margin.

Description. Shell large, inequilateral, ham-shaped, weakly inflated; dorsal margin long and straight, antero-ventral margin concave, posterior margin regularly rounded; beak obtuse and terminal; carina well defined, present on anterior part of shell, fading out distally; at least 40 radial ribs with rounded crests, regularly intercalated, getting broader towards posterior margin, straight on dorsal part of valve but curved on ventral part, interspaces as broad as or slightly broader than ribs, getting broader towards posterior margin; internal structures unknown.

Remarks. Because of the ham-shaped outline and a medial carina that was only present during early ontogeny, we assign this specimen to *Atrina* (see above). So far, *Atrina* was reported from the Triassic only by Waller & Stanley (2005) and Stiller (2001). In contrast to the Dobrogea species, *Atrina sinuata* Waller & Stanley, 2005 possesses commarginal ridges. Stiller (2001; p. 277) mentions *Atrina* n. sp. A from the Leidapo Member (late Pelsonian – early Illyrian, China), without providing a description, but judging from the described material that he assigns to this species, it lacks the numerous radial ribs that characterize *Atrina multicostata*.

The sculpture of *Atrina multicostata* is reminiscent of the Jurassic *Stegoconcha* Böhm, 1907, a genus that is closely related to *Atrina* but differs, among other things, in being higher than long.

Ecology. *Atrina* is a semi-infaunal suspension-feeder that is byssally attached to coarse sediment particles. However, in contrast to *Pinna* that lives with two-thirds of its shell into the sediment, *Atrina*

lives almost completely buried (Garcia-March *et al.* 2008). This mode of live is also assumed for Mesozoic species of that genus (Ros-Franch *et al.* 2014).

Genus PINNA Linnaeus, 1758

Type species. *Pinna rudis* Linnaeus, 1758.

Pinna simionescui n. sp.

Figure 3G

LSID. urn:lsid:zoobank.org:act:1A562F69-FB98-45FD-98F4-4DF4B6E1FE9E

Derivation of name. *Simionescui*, after the Romanian palaeontologist Ion Simionescu, for his contribution to the Triassic of North Dobrogea.

Holotype. LPB IIIL 2006

Material. One RV.

Diagnosis. *Pinna* with regularly arranged commarginal shell folds.

Description. Shell medium sized, inequilateral, subtrigonal, retrocrescent, moderately inflated at the anterior part of the valve and becoming flatter towards posterior margin; dorsal margin straight, ventral margin concave; beak terminal and acute; carina well developed in anterior part of the shell but fading away in the posterior part, separating valve into two parts of approximately equal size; regular commarginal shell folds; internal structures unknown.

Remarks. Because of the wedge- to slightly ham-shaped outline and a medial carina that was present during most of the ontogeny we assign this species to *Pinna* (see above). *Pinna yunnanensis* Chen, 1976 from the Middle and Late Triassic of China is similar in the presence of commarginal folds; however, these are broader and stronger developed compared to the Dobrogea specimen. Moreover, *P. yunnanensis* differs from the Dobrogea specimen by its straight ventral margin, resulting in a cuneiform shape, and by a continuously developed carina. *Pinna mileensis* Guo, 1985 is another pinnid with commarginal ribs that was reported from the Middle Triassic of China. In contrast to *Pinna simionescui*, the commarginal ribs of *P. mileensis* are finer but higher. Furthermore, the ventral margin is straight and the carina is continuously developed. All other Triassic species of this genus, e.g. *P. ecki* Picard, 1907, *P. meriani* Winkler, 1859, *P. tommasii* von Wöhrmann & Koken, 1892 and *P. vomis* Winkler, 1859, differ significantly in their sculpture from the Dobrogea specimen, which we therefore describe as a new species.

Ecology. Species of the genus *Pinna* are semi-infaunal suspension-feeders that are byssally attached to larger sediment particles (Cox *et al.* 1969; McRoberts 2017).

Pinna? cf. *raibliana* Parona, 1889

Figure 3I

cf. *1889 *Pinna raibliana*; Parona, p. 105, pl. 8, fig. 11.

cf. 1923 *Pinna raibliana* Parona; Diener, p. 87 [cum syn.].

cf. 1966 *Pinna* (*Pinna*) *raibliana* Parona; Allasinaz, p. 649, pl. 41, fig. 15.

cf. 1979 *Pinna raibliana* Parona; Lieberman, p. 100, pl. 4, fig. 8.

Material. One fragmented internal mould, probably from a RV.

Description. Shell medium sized, elongated, cuneiform and relatively flat; at least six radial ribs.

Remarks. Based on the ornamentation, the Dobrogea specimen could belong to *Pinna raibliana* that possesses 13 to 15 radial and nodose ribs on its dorsal parts. *P. raibliana* was described as strongly inflated (Parona 1889), which cannot be verified in the incomplete specimen from Dobrogea. Although the radial ribs indicate a wedge-shaped outline, the incomplete preservation prevents us from confirming the presence or absence of a medial carina. Our taxonomic assignment is therefore tentative. *Pinna*? cf. *raibliana* differs from *Pinna simionescui* by the presence of radial sculptural elements and the absence of commarginal shell folds.

Ecology. Same as for *Pinna simionescui*.

Occurrence. Acquate (Italy, Julian; Parona 1889), Sella delle Cave (Italy, Julian; Allasinaz 1966), Conzen Formation (Italy, Julian; Lieberman 1979), Valletta di Rogno (Italy, Carnian; Allasinaz 1972).

Superfamily POSIDONIOIDEA Neumayr, 1891

Family POSIDONIIDAE Frech, 1909

Genus BOSITRA de Gregorio, 1886

Type species. *Posidonia ornati* Quenstedt, 1851 in Quenstedt 1851–1852.

Bositra wengensis (Wissmann, 1841)

Figure 3F

*1841 *Posidonomya wengensis*; Wissmann, p. 23, pl. 16, fig. 12.

1858 *Posidonomya wengensis* Wissmann; Stoppani, p. 95, pl. 19, fig. 12.

1865 *Posidonomya wengensis* Wissmann; Laube, p. 76, pl. 20, fig. 12.

1889 *Posidonomya wengensis* Wissmann; Parona, p. 106, pl. 8, fig. 10.

1904 *Posidonia wengensis* mut. nov. *alta* (Wissmann); Frech, p. 16, fig. 15.

1923 *Posidonia wengensis* (Wissmann); Diener, p. 64 [cum syn.].

1976 *Posidonia wengensis* (Wissmann); Gu *et al.*, pl. 34, figs 32–34.

1981 *Posidonomya wengensis* Wissmann; Zardini , pl. 21, figs 7–8.

2003 *Posidonia wengensis* (Wissmann); Szente & Vörös, p. 127, pl. Biv-I, figs 27–28 [cum syn.].

Material. One RV.

Description. Shell small, thin, ovate, longer than high, weakly inflated, infracrescent, nearly equilateral; beak orthogyrate, obtuse, not projecting above straight dorsal margin; dorsal margin without auricles, antero-dorsal margin slightly shorter than posterior one; regular commarginal ribs.

Remarks. '*Daonella*" *boeckhi* Mojsisovics, 1874 is morphologically similar, but possesses a radial ornamentation in addition to commarginal ribs. The outline, presence of commarginal ribs, absence of a radial ornamentation and absence of auricles are diagnostic features of *Bositra*.

Ecology. Several modes of life have been suggested for *Bositra*, such as pseudoplanktonic (Stanley 1972), nektoplanktonic (Jefferies & Minton 1965; Hayami 1969; Duff 1975) or benthic (Conti & Monari 1992; Etter 1996). Etter (1996) showed that a benthic mode of life is most likely, and provided arguments against a pseudoplanktonic or nektoplanctonic mode of life. Since no byssal notch has been observed, Waller & Stanley (2005) suggested a reclined mode of life for *Bositra*.

Occurrence. Leidapo Member (China, late Pelsonian – early Illyrian; Komatsu *et al.* 2004), Felsőörs Formation (Hungary, Pelsonian–Illyrian; Szente & Vörös 2003), Nam Tham Formation (Vietnam, early Ladinian; Vu Khuc 2000), Cassian Formation (Italy, Longobardian–Julian; Laube 1865; Bittner 1895;

Zardini 1981), Esino Limestone (Italy, Ladinian; Stoppani 1858), Muong Trai Formation (Vietnam, Ladinian; Vu Khuc 2000), Hon Nghe Formation (Vietnam, Ladinian; Vu Khuc 2000), Hong Hoi Formation (Thailand, Ladinian; Vu Khuc 2000), Jiangdonggou Formation (China, Middle Triassic; Gu *et al.* 1976), Cataloi Formation (Romania, Ladinian–Carnian; Turculeţ 2009), Acquate (Italy, Julian; Parona 1889).

Superfamily PTERIOIDEA Gray, 1847

Family PTERIIDAE Gray, 1847

Genus PTERIA Scopoli, 1777

Type species. *Mytilus hirundo* Linnaeus, 1758.

Remarks. The general morphology of the following species is indicative for the Pteriidae as well as the Bakevelliidae. A definite assignment to one of these families is not possible because the internal shell morphology including hinge and ligament is unknown. We assign it to *Pteria* because this corresponds to its original assignment to '*Avicula*' (= *Pteria*).

Pteria sturi (Bittner, 1895)

Figures 3J–K

1865 *Avicula gea* d'Orbigny; Laube, p. 50, pl. 16, fig. 9.

1889 *Avicula gea* d'Orbigny; Parona, p. 93, pl. 8, fig. 7.

*1895 *Avicula sturi*; Bittner, p. 69, pl. 8, figs 1–4.

1923 *Avicula sturi* Bittner; Diener, p. 25 [cum syn.].

1966 *Pteria sturi* (Bittner); Allasinaz, p. 652, pl. 42, figs 4–8 [cum syn.].

1979 *Pteria sturi* (Bittner); Lieberman, p. 96, pl. 3, fig. 5 [cum syn.].

1981 *Arcavicula sturi* (Bittner); Zardini, pl. 8, fig. 15–16; pl. 10, figs 8–9.

2004 *Pteria* cf. *sturi* (Bittner); Komatsu *et al.*, fig. 7(5).

2010 *Pteria sturi* (Bittner); Komatsu *et al.*, figs 4(2–4).

Material. Four LVs.

Description. Shell medium sized, pteriiform, longer than high, oblique, weakly inflated; beak of LV acute, prosogyrate, slightly projecting above straight and long dorsal margin; anterior auricle small and not well demarcated from glank; shell margin folded inward below anterior auricle, forming a byssal gape; posterior wing long, posteriorly pointed, demarcated from flank by deep furrow; elongated groove on posterior wing running subparallel to the dorsal margin; growth lines of variable strength.

Remarks. As noted by Bittner (1895, p. 69), the specimens described as *Avicula gea* d'Orbigny, 1849 by Laube (1865) and subsequent authors belong to a different species, for which he introduced the new name *Avicula sturi*. The features of the Dobrogea specimen match those of *Avicula sturi* as described by Bittner (1895) and Allasinaz (1966), particularly with regard to shell shape, pointed posterior wing and presence of a furrow that extends below the postero-dorsal margin.

Ecology. Recent species of the genus *Pteria* live epibyssate, preferentially attached to corals (Stanley 1970, 1972) and plants (Cox *et al.* 1969, figs. 87–88). However, no corals or plants are reported from the *Tubiphytes*-microbial buildup, thus it is uncertain whether the Dobrogea specimens were attached to such organisms or to some other kind of hard substratum.

Occurrence. Leidapo Member (China, late Pelsonian – early Illyrian; Komatsu *et al.* 2004), Na Khuat Formation (North Vietnam, Anisian–Ladinian; Komatsu *et al.* 2010), Cassian Formation (Italy, Longobardian–Julian; Bittner 1895; Fürsich & Wendt 1977; Zardini 1981), Sella delle Cave (Italy, Julian; Allasinaz 1966), Rio del Lago Formation (Italy, Upper Julian; Lieberman 1979), Tor Formation (Italy, Upper Julian–Tuvalian; Lieberman 1979).

Pteria cf. *cassiana* (Bittner, 1895)

Figure 3N

cf. *1895 *Avicula cassiana*; Bittner, p. 71, pl. 8, figs 6–8.

cf. 1923 *Avicula cassiana* Bittner; Diener, p. 18 [cum syn.].

cf. 1976 *Pteria cassiana* (Bittner); Qihong *et al.*, pl. 27, figs 40–42, 45–46.

cf. 1981 *Arcavicula cassiana* (Bittner); Zardini, pl. 10, figs 11a–b.

Material. One incompletely preserved interior mould of a RV with some shell remains.

Description. Shell medium sized, pteriiform, approximately as long as high, weakly inflated; dorsal margin straight and long; anterior auricle not preserved, posterior auricle elongated, acute, with broad and shallow sinus; more or less regular growth lines.

Remarks. The outline of this taxon is almost identical to that of *Avicula cassiana* Bittner, 1895. However, the presence of up to three commarginal ribs on its posterior auricle that characterizes *A. cassiana* cannot be verified in the Dobrogea specimen. The difference between this species and *Pteria sturi* is the broader and shallower sinus below the posterior auricle in *P. sturi*. Furthermore, *P.* cf. *cassiana* is more upright than *P. sturi*.

Ecology. Same as for *Pteria sturi*.

Occurrence. Leidapo Member (China, late Pelsonian – early Illyrian; Stiller 2001; Komatsu *et al.* 2004), Cassian Formation (Italy, Longobardian–Julian; Bittner 1895; Fürsich & Wendt 1977; Zardini 1981), Weiyuanjiang Formation (China, Carnian; Qihong *et al.* 1976).

Pteria sp. A

Figure 3L

Material. One fragmented LV and one incompletely and strongly recrystallized RV.

Description. Shell medium sized, pteriiform, longer than high, weakly inflated, inflation strongest at umbonal region and flat at postero-ventral region; beak acute, prosogyrate, slightly projecting above straight and long dorsal margin; anterior auricle not observed, posterior auricle larger, triangular, not pointed.

Remarks. The incomplete preservation of the specimen prevents a determination at the species level. The specimen is similar to *Pteria sturi* but the posterior wing lacks the pointed distal end that characterizes this species.

Ecology. Same as for all other *Pteria* species.

Pteria sp. B

Figure 3M

Material. One partly preserved RV.

Description. Shell medium sized, pteriiform, strongly inflated; beak terminal, acute, prosogyrate, slightly projecting above straight dorsal margin; posterior auricle well demarcated from body shell; radial lines and growth lines.

Remarks. The outline and general features of this specimen are reminiscent of *Gervilleia*? *ogilviae* Bittner, 1895, including the presence of radial lines and growth lines, but the growth lines of *G.*?

ogilviae are stronger and not as numerous as in the Dobrogea specimen. Bakevellidae indet. reported from Foster *et al.* (2019; Fig. 7F) also possesses radial ribs, but this taxon is represented by an incompletely preserved specimen and does not allow a detailed comparison. *Pteria* sp. B differs from the other Dobrogea *Pteria* species by the radial sculptural elements and the stronger inflation.

Ecology. Same as for all other *Pteria* species.

Family BAKEVELLIIDAE King, 1850

Genus CULTRIOPSIS Cossmann, 1904

Type species. *Gervillia* (*Cultriopsis*) *falciformis* Cossmann, 1904.

Cultriopsis sp.

Figure 4A

Material. One incompletely preserved LV.

Description. Shell medium sized, lanceolate, retrocrescent, inequilateral; beak acute, prosogyrate, terminal; irregular growth lamellae on ventral margin; anterior part incompletely preserved.

Remarks. In spite of its incomplete preservation, this specimen shows the distinctive shape of *Cultriopsis*. However, a determination at the species level is impossible because the posterior auricle is not preserved.

Ecology. Byssally attached epifaunal suspension-feeder (Hautmann 2001*a*).

Genus GERVILLARIA Cox, 1954

Type species. *Modiola*? *alaeformis* J. Sowerby, 1819.

Gervillaria subelegans (Chen in Gu *et al.,* 1976)

Figures 4B–C

*1976 *Bakevelloides subelegans*; Chen, p. 136, pl. 27, figs 8–9.

1976 *Bakevelloides subelegans* Chen; Qihong *et al.*, pl. 28, fig. 38.

2004 *Gervillaria subelegans* (Chen); Komatsu *et al.*, p. 216, fig. 7(4).

Material. Three LVs.

Description. LV medium to large in size, higher than long, retrocrescent, strongly inflated, bialate; beak prosogyrate, acute, rising prominently above straight dorsal margin; anterior auricle weakly

demarcated from main body of shell, posterior auricle larger than anterior one, better demarcated from main body of shell by sulcus and steep diagonal carina; regular growth lines on the entire surface of shell.

Remarks. Although the internal characters of the Dobrogea specimens are unknown, they agree very well with *Gervillaria subelegans*, as illustrated in Komatsu *et al.* (2004), in terms of size, overall morphology and ornamentation.

Ecology. *Gervillaria* has been interpreted as an epifaunal or semi-infaunal recliner (Muster 1995, p. 99; Aberhan & Muster 1997).

Occurrence. Leidapo Member (China, late Pelsonian – early Illyrian; Stiller 2001; Komatsu *et al.* 2004), Yunnan (China, Middle Triassic; Qihong *et al.* 1976).

Genus UNCERTAIN

Bakevelliidae indet.

Figure 4D

Material. One incompletely preserved LV.

Description. Shell large, pteriiform, longer than high, strongly inflated; beak prosogyrate, projecting above straight dorsal margin; anterior auricle not preserved, posterior auricle well demarcated from flank.

Remarks. The shape and the strong inflation indicate that this specimen belongs to the Bakevelliidae, but due to incomplete preservation a more accurate determination is not possible.

Ecology. Probably the same as for *Gervillaria subelegans*.

Suborder PECTININA Waller, 1978

Superfamily AVICULOPECTINOIDEA Meek & Hayden, 1865

Family UNCERTAIN

Remarks. The two taxa described below have a pectinoid shape but lack a ctenolium, which is a key character of Pectinoidea in the strict sense (Waller 1984; Hautmann 2010). We therefore assign these taxa to the Aviculopectinoidea *s. l.*, which corresponds to the hyporder Aviculopectinoidei excluding the Pterinopectinoidea in the classification of Carter *et al.* (2011). Although Aviculopectinoidei is heavily oversplit, the combination of characters observed in these taxa does not conform to the character set of any available genus. This problem raises the general question of classification in a clade that is characterized by extreme morphological convergence, plasticity, and mosaic evolution, which is beyond the scope of the present paper. We therefore present these taxa in open nomenclature and will discuss their taxonomy in a future study.

‘*Pecten*’ *volaris* (Bittner, 1902)

Figure 4H

*1902 *Pecten volaris*; Bittner, p. 634, pl. 27(10), fig. 32.

1972 *Chlamys* (*Chlamys*) *volaris* (Bittner); Allasinaz, p. 339, pl. 44, fig. 9; pl. 45, figs 1–2.

1981 cf. *Chlamys volaris* (Bittner); Zardini, pl. 18, figs 8a–b.

Material. One LV and one internal mould of a LV.

Description. Shell small to medium sized, suborbicular, slightly longer than high, strongly inflated, equilateral; dorsal margin short and straight; beak acute, orthogyrate and slightly projecting above dorsal margin; auricles incompletely preserved but clearly demarcated from disc; incremental lines on anterior auricle indicate presence of deep byssal notch; ctenolium absent; 18 strong radial plicae equal in strength, with regularly arranged tubercles at top of steep crests, starting close to beak, ribs on distal part of disc slightly curved, posterior auricle showing commarginal ribs, interspaces between ribs broad and deep.

Remarks. *Chlamys*-like bivalves were diverse in the Middle and Late Triassic, but their generic assignment is often doubtful. One example is represented by Bittner’s (1902) *Pecten volaris*, subsequently assigned to *Chlamys* by Allasinaz (1972). As noted by Bittner (1902, p. 635), this species is unusual among morphologically similar forms from the Triassic for having a strongly vaulted RV. Bittner (1902) concluded that this species might have given rise to ‘*Vola*’ (= *Pecten*) -like taxa in the

Jurassic, which have generally a RV that is stronger vaulted in comparison to the LV. However, '*Pecten*' *volaris* lacks a ctenolium and therefore cannot be attributed to *Pecten* or *Chlamys*.

The specimens from Dobrogea agree very well with all main features of *Pecten volaris* as described by Bittner (1902) and revised by Allasinaz (1972). However, neither Bittner (1902) nor Allasinaz (1972) mentioned regularly arranged tubercles at the top of the rib crests, which are also not visible on the figures provided by these authors. We ascribe this lack of tubercles to an incomplete preservation.

Ecology. Epibyssate suspension-feeders that rested pleurothetically on their RVs.

Occurrence. Cassian Formation (Italy, Longobardian–Julian; Zardini 1981), Gajine by Čevljanovići (Bosnia and Herzegovina, Julian; Bittner 1902; Allasinaz 1972).

Aviculopectinoidea n. gen. et n. sp.

Figures 4E–G

Material. Two RVs and one LV.

Description. Shell medium sized, infracrescent, both valves strongly inflated, suborbicular, higher than long, subequilateral; umbo orthogyrate; beak acute, located in the middle of the straight dorsal margin and slightly projecting above it; auricles clearly demarcated from disc, posterior auricles obtuse; RV (Figs 4E and 4G): anterior auricle elongated, acute, with deep byssal notch lacking a

ctenolium; LV (Fig. 4F): anterior auricle triangular with small byssal sinus; faint antimarginal lines and growth lines on disc, where preserved; anterior auricle externally covered with slightly irregular commarginal ribs; internal structures unknown.

Remarks. The strongly inflated RV resembles '*Pecten*' *volaris* described above, but the new taxon lacks the pronounced radial plicae that characterize the latter species. A very unusual feature is the strong and approximately equal inflation of both valves, because pectinoid and aviculopectinoid bivalves usually have differentially vaulted valves, with at least one valve being flatter than in this taxon. Because the LV of '*Pecten*' *volaris* is unknown, it is unclear whether the two taxa differ in this respect.

Ecology. The deep byssal notch suggests that this species was an epibyssate suspension-feeder, but the equally inflated valves contradict a pleurothetic mode of life, which is common in pectinoids and aviculopectinoids. We therefore assume an orthothetic mode of life for these specimens.

Family ANTIJANIRIDAE Hautmann in Carter *et al.*, 2011

Genus AMPHIJANIRA Bittner, 1901

Type species. *Pecten janirula* Bittner, 1895.

Amphijanira? aff. *landrana* (Bittner, 1895)

Figures 4J–K

aff. *1895 *Pecten landranus*; Bittner, p. 166, pl. 19, fig. 21.

aff. 1972 *Amphijanira*? *landrana* (Bittner); Allasinaz, p. 269, pl. 33, figs 3–5 [cum syn.].

aff. 1981 *Amphijanira*? *landrana* (Bittner); Zardini, pl. 18, figs 4–5, 9a–b.

Material. Two incompletely preserved LVs and one questionable LV.

Description. Shell medium sized, infracrescent, equilateral, higher than long, weakly inflated; beak acute and orthogyrate; auricles not preserved; radial ribs with rounded crests, approximately 20 first order ribs starting close to beak, second order ribs irregularly intercalated, third and fourth order ribs occasionally present, similar in strength than second order ribs, higher order ribs closer to first order ribs than to second order ribs, interspaces between first order ribs broadest in the middle of disc where ribs of different orders can be easily distinguished from each other, at the anterior and posterior part of the disc interspaces between first order ribs smaller and second order ribs rarely intercalated, higher order ribs missing in these parts, fine and regular growth lines forming small nodes on the flanks of ribs where crossing them.

Remarks. The Dobrogea specimens might represent an ancestor of *Pecten landrana* Bittner, 1895, a Carnian bivalve revised by Allasinaz (1972). The sculpture of the LV of *P. landrana* is similar to the Dobrogea specimens. However, the ribs of the Dobrogea specimens are thicker. Allasinaz (1972) provisionally assigned *Pecten landrana* to the genus *Amphijanira*, which is followed herein.

Ecology. Species of the genus *Amphijanira* were probably epibyssate suspension-feeders (Ros-Franch *et al.* 2014).

Family HETEROPECTINIDAE Beurlen, 1954

Genus NEOMORPHOTIS Yin & Yin, 1983

Type species. *Neomorphotis gigantea* Yin & Yin, 1983.

Neomorphotis comta (Goldfuss, 1833 in Goldfuss 1833–1841)

Figures 4L–N

*1833 *Ostrea comta*; Goldfuss, p. 4, pl. 72, fig. 6.

1835 *Spondylus comtus* (Goldfuss); Goldfuss, p. 93, pl. 105, fig. 1

1900 *Pseudomonotis beneckei*; Bittner, p. 574, pl. 23, fig. 5.

1923 *Prospondylus comptus* (Goldfuss); Diener, p. 122 [cum syn.].

1926 *Prospondylus comptus* (Goldfuss); Reis, p. 124, pl. 9, figs 12–14.

1937 *Prospondylus comtus* (Goldfuss); Assmann, p. 58, pl. 12, fig. 1.

1967 *Prospondylus* cf. *comptus* (Goldfuss); Speciale, p. 1105, pl. 82, fig. 2 [cum syn.].

2008 *Neomorphotis compta* (Goldfuss); Posenato, p. 101, figs 4A–G [cum syn.].

Material. 22 LVs, one RV, two articulated specimens and probably six additional specimens with unknown orientation. Specimens mostly incomplete.

Description. Shell large to very large, infracrescent, inequivalve, inequilateral, supposedly higher than long, antero-dorsal margin shorter than postero-dorsal one; beaks prosogyrate; LV: inflated; beak projecting above dorsal margin; anterior auricle smaller than posterior wing, obtuse, relatively well demarcated from umbonal region, no byssal sinus; posterior wing faintly demarcated from umbonal region, never completely preserved but probably obtuse; RV: less inflated than LV; beak not projecting above dorsal margin; anterior auricle elongated, clearly demarcated from umbonal region by deep byssal notch; LV possesses five to seven strong first order ribs with tubercules, starting close to beak, second order ribs regularly intercalated in centre of first order interspaces, significantly weaker than first order ribs, sometimes with small tubercles, four to six additional ribs of subordinate order occur, ribs partly visible on internal moulds, fine growth lines occasionally preserved, sculpture of RV generally stronger than in LV, first order ribs strongest in posterior region and decreasing in strength anteriorly, hardly distinguishable in the middle and the anterior region from higher order ribs, tubercles only visible on the strong first order ribs in the posterior region, second order ribs starting closely to the beak, one to three third order ribs irregularly intercalated.

Remarks. The original specific name *comta* introduced by Goldfuss (1833) was corrected by Frech (1909) to *compta*, because Frech considered *comta* to be an inadvertent spelling error. However, 'comtus' was commonly used in the sense of 'ornate' in Goldfuss' time (e.g. Doederlein 1829, p. 259), thus Goldfuss had chosen this word by intention and the correction of Frech (1909) is unjustified. Posenato (2008) provided a detailed discussion of *Neomorphotis comta*, to which the reader is referred.

Ecology. The byssal notch suggests that these bivalves were epibyssate suspension-feeders that rested pleurothetically on their RVs.

Occurrence. Jena Formation (Germany, late Bithynian – early Illyrian; Assmann 1937), Karlstadt Formation, Heilbronn Formation, Diemel Formation (Germany, early Illyrian; Assmann 1937), Dont Formation (Italy, Pelsonian–Illyrian; Posenato 2008), Valle Sabbia (Italy, middle Anisian; Speciale 1967), Wetterstein Limestone (Austria, Ladinian; Reis 1926).

Family ASOELLIDAE Begg & Campbell, 1985

Genus ASOELLA Tokuyama, 1959

Type species. *Eumorphotis* (*Asoella*) *confertoradiata* Tokuyama, 1959.

Asoella? sp.

Figure 4I

Material. One incompletely preserved LV.

Description. Shell small, subcircular, slightly longer than high, moderately inflated; dorsal margin short, probably lacking well-differentiated auricles; beak small, obtuse, broadly rounded, orthogyrate, slightly projecting above dorsal margin; weak and regular growth lines, best visible at shell margins.

Remarks. The subcircular shape, position of the beak, shell inflation, and the probable lack of well-differentiated auricles in the LV are indicative for the genus *Asoella*. However, incomplete preservation and the absence of information on the shell interior and the morphology of the RV make this assignment provisional.

Ecology. The shallow byssal notch in *Asoella* (Cox *et al.* 1969; not observed in the present material) indicates an epibyssate mode of life.

Genus LEPTOCHONDRIA Bittner, 1891

Type species. *Pecten aeolicus* Bittner, 1891.

Leptochondria pervulgata (Bittner, 1902)

Figures 5A–B

*1902 *Pecten* (?*Entolium*) *pervulgatus*; Bittner, p. 609, pl. 26, fig. 25.

1972 *Leptochondria pervulgata* (Bittner); Allasinaz, p. 248, pl. 30, figs 2–4.

Material. 15 LVs and possibly two fragmented LVs.

Description. Shell medium sized, equilateral, subcircular, slightly longer than high, weakly inflated; beak orthogyrate, positioned in the middle of straight dorsal margin and not projecting above it; auricles faintly demarcated from disc, obtuse, sub-equal in size; approximately 20 to 25 widely spaced ribs of first and second order with rounded crests, first order ribs starting close to the beak, second order ribs slightly weaker, starting shortly below beak, regularly intercalated, few third order ribs present, very weak and irregularly inserted by intercalation, ribs strongest in the middle part of the disc and near the ventral margin, weaker at the anterior and posterior margins, auricles without radial ribs, but fine and regular growth lines visible to the naked eye, most clearly on distal parts of disc and auricles.

Remarks. The specimens from Dobrogea agree very well with all main features of *Leptochondria pervulgata* as described by Bittner (1902) and revised by Allasinaz (1972). Bittner (1902) reported 25 to 30 ribs (or even more) that are irregularly distributed, resulting in an irregular pattern of stronger and weaker ribs. This irregular pattern probably results from the irregularly intercalated third order ribs. In contrast, Allasinaz (1972) described the thinner second order ribs to be regularly intercalated between the first order ribs, but he did not mention any ribs of third order. However, the specimens shown in Allasinaz (1972), which are the original specimens of Bittner (1902), show irregularly intercalated third order ribs, which occur also in the Dobrogea specimens. Only one specimen shown in Allasinaz (1972) possesses two completely preserved auricles that are sub-equal in size, which is also the case in the Dobrogea specimens.

Ecology. Specimens of this genus have a flat RV with a byssal notch (not observed in the present material), suggesting that these bivalves were epibyssate suspension-feeders that rested pleurothetically on their RVs (Hautmann *et al.* 2013; Hofmann *et al.* 2014).

Occurrence: Clade near Čevljanovići (Bosnia and Herzegovina, Anisian; Bittner 1902), Monte Rite (Italy, Anisian; Allasinaz 1972).

Leptochondria separata (Reis, 1926)

Figures 5C–D

*1926 *Pecten separatus*; Reis, p. 122, pl. 9, fig. 9.

1972 *Leptochondria separata* (Reis); Allasinaz, p. 251, pl. 30, fig. 8 [cum syn.].

Material. Four LVs and one questionable LV.

Description. Shell small, subcircular and slightly higher than long, weakly inflated, more or less equilateral; beak orthogyrate, positioned in the middle of straight dorsal margin and slightly projecting above it; auricles not well demarcated from disc, obtuse, probably equal in size, broad but shallow byssal sinus below anterior auricle; up to 27 radial ribs on disc, intercalated in two ranks, first order ribs starting close to beak, increasing in strength towards the ventral margin, crests rounded, second order ribs irregularly intercalated, growth lines very weak, auricles occasionally ornamented with weak radial ribs and growth lines, growth lines most clearly developed on auricles.

Remarks. The lectotype, refigured in Allasinaz (1972), shows a broad but shallow byssal sinus, which is also present in the material from Dobrogea. *Leptochondria separata* differs from *Leptochondria*

pervulgata by its smaller size, a more obtuse beak projecting above the dorsal margin, a higher number of more densely spaced ribs and weaker growth lines.

Ecology. Same as for *Leptochondria pervulgata*.

Occurrence. Wetterstein Limestone (Austria, Ladinian; Reis 1926, Allasinaz 1972).

Leptochondria viezzenensis (Wilckens, 1909)

Figures 5F–H

*1909 *Pecten viezzenensis*; Wilckens, p. 147. pl. 5, fig. 25.

1972 *Leptochondria viezzenensis* (Wilckens); Allasinaz, p. 259, pl. 31, figs 5–9.

2003 *Leptochondria* cf. *viezzenensis* (Wilckens); Szente & Vörös, p. 128, pl. Biv-II, figs 9–11.

2012 *Leptochondria viezzenensis* (Wilckens); Wasmer *et al.*, p. 1058, figs 7 (K–R).

Material. Four well preserved LVs and one poorly preserved LV.

Description. LV small to medium sized, infracrescent, subcircular, longer than high, equilateral, weakly inflated; beak obtuse, orthogyrate, positioned in the middle of straight dorsal margin and slightly projecting above it; auricles faintly demarcated from disc, anterior auricle obtuse and slightly larger than posterior one, posterior auricle with shallow sinus; up to 40 ribs of three orders with

rounded crests, interspaces broader than ribs, thin first order ribs regularly arranged, starting close to beak, second order ribs regularly intercalated, starting a few mm below the beak and almost as broad as first order ribs, few third order ribs irregularly intercalated in the middle part of the disc, ribs on auricles weaker developed than on the disc, fine and regularly growth lines visible on disc and auricles.

Remarks. The Dobrogea specimens match very well with the features of *Leptochondria viezzenensis* described in Wilckens (1909), Allasinaz (1972) and Wasmer *et al.* (2012). However, Wilckens (1909) mentioned that the growth lines on the auricles are more distinct than those on the disc, which is not the case in the Dobrogea specimens. Furthermore, Allasinaz (1972) describes the ribs as irregularly intercalated, which is only the case for the third order ribs of the Dobrogea specimen. However, in all other points the characters of *L. viezzenensis* match those of the Dobrogea specimens. According to Wasmer *et al.* (2012, p. 1059) also *Leptochondria minima* (Kiparisova, 1938) and *Leptochondria virgalensis* (von Wittenburg, 1909) may possess a shallow sinus in the left posterior auricle, but the sculptures of these species differ clearly from the sculpture of *L. viezzenensis*. In contrast to *Leptochondria pervulgata*, which is also longer than high, *L. viezzenensis* possesses a beak that is slightly projecting above the dorsal margin, ribbed auricles, a posterior auricle with a shallow sinus and a higher number of ribs.

Ecology. Same as for all other *Leptochondria* species.

Occurrence. Mianwali Formation (Pakistan, late Smithian – middle Spathian; Wasmer *et al.* 2012), Felsőörs Formation (Hungary, Pelsonian–Illyrian; Szente & Vörös 2003), Cima Viezzena (Italy, Longobardian; Wilckens 1909; Allasinaz 1972).

Family ORNITHOPECTINIDAE Hautmann in Carter *et al.*, 2011

Genus ORNITHOPECTEN Cox, 1962

Type species. *Aviculopecten bosniae* Bittner, 1902.

Ornithopecten interruptus (Bittner, 1902)

Figure 5I

*1902 *Aviculopecten interruptus*; Bittner, p. 591, pl. 26, fig. 13.

1972 *Ornithopecten interruptus* (Bittner); Allasinaz, p. 263, pl. 32, fig. 5.

Material. One well preserved LV.

Description. Shell medium sized, infracrescent, longer than high, inequilateral, weakly inflated; beak acute, orthogyrate, slightly projecting above straight dorsal margin, postero-dorsal margin more than twice as long as antero-dorsal margin; posterior wing elongated and flat, anterior auricle smaller than posterior wing, growth lines on wing and auricle suggestive of acute distal ends, shallow byssal sinus below anterior wing; approximately 22 rounded ribs that are straight on the posterior part of the shell but curved on the anterior part, approximately 10 first order ribs starting close to beak, separated by broad interspaces, one first order rib coinciding with the postero-dorsal margin, second

order ribs starting at various distances from the beak, irregularly intercalated, regular growth lines reflected by slight elevations on shell.

Remarks. Bittner (1902) and Allasinaz (1972) describe *Ornithopecten interruptus* as medium sized, suborbicular and weakly inflated bivalve that is longer than high and has an elongated posterior wing that is larger than the anterior auricle. Both structures have acute distal ends and are poorly demarcated from the disc. The Dobrogea specimen is in accordance with all these characters and also shows high similarities to the sculpture of *O. interruptus*. Bittner (1902) reported six growth disruptions that interrupt and shift the radial ribs. We regard this feature as a response to environmental changes rather than a character of taxonomic importance. We follow Cox (1962) and assign this species to the genus *Ornithopecten*.

Ecology. Specimens of the genus *Ornithopecten* have a less inflated RV with a byssal notch (not observed in the present material), suggesting that these bivalves were epibyssate suspension-feeders that rested pleurothetically on their RVs.

Occurrence. Clade near Čevljanovići (Bosnia and Herzegovina, Anisian; Bittner 1902; Allasinaz 1972).

Ornithopecten cf. *katzeri* (Bittner, 1902)

Figure 5E

cf. *1902 *Aviculopecten katzeri*; Bittner, p. 608, pl. 26, fig. 22.

cf. 1972 *Ornithopecten katzeri* (Bittner); Allasinaz, p. 263, pl. 32, fig. 4.

Material. One almost completely LV.

Description. Shell small, ovate, inequilateral, weakly inflated; beak prosogyrate, acute; antero-dorsal margin straight and probably longer than postero-dorsal margin; wings faintly demarcated from disc, anterior wing small; seven first order ribs, starting close to beak, generally separated by broad interspaces, ribs slightly curved, rib interspaces on anterior part narrower than on posterior part, up to five thin second order ribs intercalated between first order ribs, weak commarginal ribs forming tubercles where they cross first order ribs.

Remarks. The Dobrogea specimen is very similar to *Ornithopecten katzeri*, which, however, is based on a single RV, which makes the assignment of the present LV uncertain. Bittner (1902) and Allasinaz (1972) mentioned a slightly higher number of ribs (ten first order ribs and up to eight second order ribs between first order ribs), which might be due to the slightly larger size of the type specimen. *O.* cf. *katzeri* can be distinguished from *Ornithopecten interruptus* by the prosogyrate beak, the lower number of first order ribs and the higher number of second order ribs.

Ecology. Same as for *Ornithopecten interruptus*.

Occurrence. Clade near Čevljanovići (Bosnia and Herzegovina, Anisian; Bittner 1902; Allasinaz 1972).

Superfamily PECTINOIDEA Rafinesque, 1815

Family PECTINIDAE Rafinesque, 1815

Genus AVICHLAMYS Allasinaz, 1972

Type species. *Pecten csopakensis* Frech, 1905.

Avichlamys? cf. *nicolensis* (Ogilvie Gordon, 1927)

Figure 5O

cf. *1927 *Pecten nicolensis*; Ogilvie Gordon, p. 26, pl. 2, fig. 22.

cf. 1972 *Avichlamys nicolensis* (Ogilvie Gordon); Allasinaz, p. 370, pl. 48, fig. 11.

Material. One incompletely preserved LV.

Description. Shell medium sized, infracrescent, almost flat; postero-dorsal part not preserved; anterior auricle incompletely preserved, well demarcated from disc; at least 16 distinct, narrow but high radial first order ribs with rounded crests, wide interspaces getting broader distally where thin second order ribs are intercalated, second order ribs positioned asymmetrically in-between first order ribs, commarginal riblets also present, creating a reticular pattern by crossing radial ribs, distance between commarginal riblets decreasing towards ventral margin.

Remarks. Two Triassic pectinoid species have an ornamentation similar to the Dobrogea specimen, namely *Pecten reticulatus* von Schlotheim, 1820 and *Avichlamys nicolensis* (Ogilvie Gordon, 1927), but the latter is weaker inflated (Ogilvie Gordon 1927). Because the Dobrogea specimen is almost flat, we provisionally assign it to *A. nicolensis*. If correct, this implies that *Avichlamys* survived into the Middle Triassic.

Ecology. Epibyssate suspension-feeder that rested pleurothetically on its RV.

Occurrence. Werfen Formation (Italy, Early Triassic; Ogilvie Gordon 1927; Allasinaz 1972).

Genus CHLAMYS Röding in Bolten, 1798

Type species. *Pecten islandicus* Müller, 1776.

Subgenus PRAECHLAMYS Allasinaz, 1972

Type species. *Pecten* (*Chlamys*) *inaequialternans* Parona, 1889.

Chlamys (*Praechlamys*) *prima* n. sp.

Figures 5J–M

LSID. urn:lsid:zoobank.org:act:6EDFD317-06D9-4492-BF45-ED9A60654390

Derivation of name. *Prima* (Latin: the first) because this species is among the geologically earliest species of its genus.

Holotype. LPB IIIL 2062

Paratypes. LPB IIIL 2060, 2061, 2063, 2064, 2065

Material. Twelve fragmented but otherwise well preserved LVs, two internal moulds of LVs with some shell remains, one external mould of a LV and one unassigned valve.

Diagnosis. *Praechlamys* with approximately 30 radial ribs arranged in two ranks on the LV; anterior disc margin demarcated from anterior auricle by steep slope; shallow radial depression on posterior part of disc, where radial ornament becomes weaker than on main part of disc.

Description. Shell medium sized, moderately inflated, inequilateral, suborbicular, approximately as high as long, disc inflation decreases towards the posterior margin, separating morphologically the posterior part from the remaining disc; beak slightly prosogyrate, positioned in the middle of the straight dorsal margin and slightly projecting above it; auricles relatively large, anterior auricle with byssal sinus and larger than posterior one, clearly demarcated from disc by steep slope, posterior auricle truncated, obtuse and smaller than anterior one, clearly demarcated from disc but slope not as steep as anteriorly; up to 30 rounded first and second order ribs bearing small tubercles, getting broader towards the ventral margin, first order ribs starting close to beak, second order ribs starting slightly more distally, regularly intercalated, ribs denser but weaker on flat posterior part of disc,

growth lines present, two weak ribs and several riblets on posterior auricle; internal structures not observed.

Remarks. The most similar species is *Chlamys* (*Praechlamys*) *subdivisa* (Bittner, 1901), which differs in having a tripartite division of the disc with a broad middle part and narrow radial depressions anteriorly and posteriorly. In the Dobrogea specimens a comparable depression/flattening of the disc occurs only posteriorly. Furthermore, *C.* (*P.*) *subdivisa* has 40 to 50 smooth ribs while *C.* (*P.*) *prima* has only approximately 30 ribs. The intercalation of second order ribs in *C.* (*P.*) *subdivisa* is more irregular and the posterior auricle lacks ribs or riblets.

Ecology. Specimens of *Chlamys* (*Praechlamys*) have a slightly less inflated RV with a deep byssal notch below the anterior auricle (as inferred from the presence of a byssal sinus in the LV). This suggests that these bivalves were epibyssate suspension-feeders that rested pleurothetically on their RVs.

Genus UNCERTAIN

Pectinidae indet.

Figures 5P–Q

Material. One LV and one RV, both incompletely preserved internal moulds.

Description. Shell small, suborbicular, subequilateral, slightly higher than long; LV weakly inflated, RV less inflated than LV; approximately ten regularly arranged, broad radial folds with narrow interspaces, irregular growth lines.

Remarks. These specimens are unlike all other pectinoids from Dobrogea with respect to their ornamentation. Because the present specimens are internal moulds, we cannot reconstruct the original ornament in detail, except from the fact that the species had ten main plicae. We therefore present this species in open nomenclature.

Ecology. The less inflated RV suggests that these bivalves were epibyssate suspension-feeders that rested pleurothetically on their RVs.

Family PLEURONECTITIDAE Hautmann in Carter *et al.*, 2011

Genus PLEURONECTITES von Schlotheim, 1820

Type species. *Pleuronectites laevigatus* von Schlotheim, 1820.

Pleuronectites? cf. *balatonicus* (Bittner, 1901)

Figure 5N

cf. *1901 *Pecten balatonicus*; Bittner, p. 37, pl. 5, figs 9–11.

? 1972 *Pleuronectites balatonicus* (Bittner); Allasinaz, p. 323, pl. 43, fig. 5 (non fig. 6).

Material. One almost complete RV and possibly one additional, incompletely preserved RV.

Description. Shell of RV small to medium sized, weakly inflated or nearly flat, inequilateral, higher than long; beak orthogyrate, positioned in the middle of straight dorsal margin and not projecting above it; auricles unequal in size, anterior auricle elongated, clearly demarcated from disc by deep byssal notch, posterior auricle obtuse, triangular, clearly demarcated from disc; shell exterior smooth except for weak, irregularly spaced incremental lines and weak radial striae that possibly represent radial sectors of the shell microstructure, as described by Carter & Hautmann (2011).

Remarks. The shape of this specimen is virtually identical to that of Bittner's (1901) type specimen of *Pecten balatonicus*, except for a relatively shorter anterior auricle. However, it seems possible that this difference is due to incomplete preservation. Although we provisionally follow Allasinaz' (1972) assignment to *Pleuronectites*, we note that this assignment is problematic. First, the presence of a ctenolium cannot be demonstrated, although this feature might be absent due to incomplete preservation. Second, the ligament morphology is unknown. The specimens from the Cassian Formation that Allasinaz (1972, pl. 34, fig. 6a–c) assigned to *P. balatonicus* do clearly not belong to *Pleuronectites* (see revision of *Pleuronectites* in Hautmann 2010) but to an entoliid species. Still, the overall morphology, smooth shell exterior and the radial arrangement of shell-microstructural features are suggestive for *Pleuronectites* (Hautmann 2010; Carter & Hautmann 2011). The outline of this specimen is also very similar to the new aviculoid taxon described above (Figs 4E–G), but its valve is nearly flat, which is not due to compaction because no deformation features are observed.

Ecology. The byssal notch in the RV suggests that this species was an epibyssate suspension-feeder that rested pleurothetically on its RVs (Hautmann 2010).

Occurrence. Veszprémer Mergel (Hungary, Carnian; Bittner 1901; Allasinaz 1972).

Suborder ENTOLIIDINA Hautmann in Carter *et al.*, 2011

Superfamily ENTOLIOIDEA von Teppner, 1922

Family ENTOLIIDAE von Teppner, 1922

Genus ENTOLIUM Meek, 1865

Type species. *Pecten demissus* Meek, 1865.

Entolium reticulatum n. sp.

Figure 5R

LSID. urn:lsid:zoobank.org:act:CADEA6B4-C9F9-41C0-8D51-BF6F62E5BA95

Derivation of name. *Reticulum* (Latin: net), referring to the reticular sculpture.

Holotype. LPB IIIL 2070

Material. Two LVs.

Diagnosis. *Entolium* with weak reticular ornamentation, resulting from thin and regular radial folds crossing commarginal folds.

Description. Shell small, disc weakly inflated, subcircular, equilateral; beak orthogyrate, located in the middle of straight dorsal margin and projecting above it, two weak depressions located at the anterior and posterior part of the disc, probably corresponding to internal lateral disc buttresses; auricles obtuse and equal in size, posterior auricle demarcated more clearly from disc than anterior one, growth lines present, no byssal sinus; thin and regular radial folds, most clearly developed on umbonal region, regular commarginal folds, almost as broad or slightly broader than radial folds, most clearly on umbonal region, radial and commarginal folds form weak reticular pattern; internal characters unknown.

Remarks. The ornamentation of this specimen is different from all Triassic entoliids known to us.

Ecology. Specimens of the genus *Entolium* lack a byssal notch, suggesting that these bivalves where unattached epifaunal suspension feeders.

Entolium sp.
Figure 5V

Material. Two LVs.

Description. Shell small, weakly inflated, inequilateral, suborbicular, higher than long; beak orthogyrate and obtuse; two radial depressions on dorsal part of disc probably corresponding to internal disc buttresses, posterior despression slightly more developed than anterior one; auricles clearly demarcated from disc, obtuse; growth lines and weak radial lines, visible on disc and auricles

Remarks. The Dobrogea specimens show similarities with *Entolium discites* (von Schlotheim, 1820) and *Entolium hallense* (von Wöhrmann, 1889) as described in Allasinaz (1972). However, the preservation state of the specimens, especially the poorly preserved auricles, prevent a clear assignment to one of these two species. Therefore we present the Dobrogea specimens in open nomenclature. *Entolium* sp. differs from *Entolium reticulatum* by the lack of the reticular ornamentation.

Ecology. Same as for *Entolium reticulatum*.

Genus ENTOLIOIDES Allasinaz, 1972

Type species. *Pecten zitteli* von Wöhrmann & Koken, 1892.

Entolioides deeckei (Parona, 1889)

Figures 5S–U

*1889 *Pecten* (*Vola*?) *deeckei*; Parona, p. 92, pl. 6, fig. 8.

1892 *Pecten deeckei* Parona; von Wöhrmann & Koken, p. 172, pl. 9, figs 1–2.

1923 *Pecten* (*Entolium*) *deeckei* Parona; Diener, p. 69 [cum syn.].

1972 *Entolioides deeckei* (Parona); Allasinaz, p. 297, pl. 37, figs 6–9 [cum syn.].

Material. Four LVs that are mostly incomplete and/or internal moulds with some shell remains. Possibly one additional LV and one incompletely preserved LV showing some details of the internal morphology.

Description. Shell large, disc longer than high, subequilateral, weakly inflated; beak obtuse, orthogyrate, not projecting above straight dorsal margin; depression subparallel to postero-dorsal margin starting close to beak occasionally present (Fig. 5S), probably reflecting internal structural elements; auricles obtuse, posterior auricle better demarcated from disc than anterior one, no byssal sinus; first and second order ribs with slightly variable interspaces, approximately 11 first order ribs starting close to beak and getting broader towards posterior margin, regularly intercalated second order ribs starting somewhat below the beak, fine, dense and regularly arranged growth lines producing irregular nodes and wavy crests on ribs, auricles with growth lines only; monomyarian, adductor muscle scar rounded and located on the postero-ventral part of the shell (Fig. 5U), ligament alivincular-alate, auricular crura present along lower border of auricles starting close to the resilifer, growth lines and first order ribs present.

Remarks. We assign the Dobrogea specimens to *Entolioides deeckei* based on size, shape and the diagnostic ornamentation.

Ecology. The byssal sinus of *Entolioides* (not preserved in the present material) is either weak or lacking and the RV is less inflated than the LV (Allasinaz 1972, table 3). This suggests that species of this genus were unattached epifaunal suspension feeders that rested pleurothetically on their RVs.

Occurrence. Schlernplateau beds (Italy, late Longobardian – early Julian; von Wöhrmann & Koken 1892; Allasinaz 1972), Acquate (Italy, Julian; Parona 1889; Allasinaz 1972), Valletta di Rogno (Italy, Carnian; Allasinaz 1972).

Genus SCYTHENTOLIUM Allasinaz, 1972

Type species. *Pecten tirolicus* von Wittenburg, 1908.

Scythentolium anisicum n. sp.

Figures 6A–D

LSID. urn:lsid:zoobank.org:act:FA7D2579-A447-47EE-A277-732EB85105A0

Derivation of name. Referring to the stratigraphic age of this species.

Holotype. LPB IIIL 2075

Paratypes. LPB IIIL 2076, 2077, 2079, 2080, 2081, 2082, 2083, 2084, 2085, 2086, 2158

Material. Eight LVs, two RVs, three articulated and four fragmentary shells.

Diagnosis. *Scythentolium* with slightly procresent disc.

Description. Shell large, disc subcircular, inequivalve, slightly procrescent; inflation of valves moderate, comparable in LV and RV; beak obtuse, orthogyrate and positioned in the middle of dorsal margin but not projecting above it; dorsal margin straight in LV and angulate in RV; auricles of LV subequal in size, obtuse, clearly demarcated from disc; auricles of RV obtuse, triangular, clearly demarcated from disc, byssal notch below anterior auricle; both valves smooth except for regular and fine growth lines and very fine antimarginal structure (Fig. 6D), growth lines and antimarginal lines also observable on auricles.

Remarks. A deep byssal notch and a smooth shell surface are characteristic for the genus *Scythentolium* Allasinaz, 1972. Because the Dobrogea specimens differ from all other Triassic *Scythentolium* species by the slightly procrescent growth, we erect a new species, *S. anisicum*. Our finds indicate that *Scythentolium* was not restricted to the Early Triassic but persisted into the Middle Triassic.

Ecology. The byssal notch of *Scythentolium* suggests that species of this genus were epibyssate suspension-feeders that rested pleurothetically on their RVs.

Suborder OSTREINA Férussac, 1822 in Férussac 1821–1822

Superfamily OSTREOIDEA Rafinesque, 1815

Family OSTREIDAE Rafinesque, 1815

Genus UMBROSTREA Hautmann, 2001*b*

Type species. *Umbrostrea emamii* Hautmann, 2001b.

Umbrostrea? sp.

Figure 6K

Material. One internal mould of a LV.

Description. Shell small, subelliptical, retrocrescent, with relatively large attachment surface and strongly plicate shell margin; plicae rounded, regularly arranged but varying in thickness.

Remarks. The curvature suggests that this specimen is a LV, which, in combination with the presence of an attachment surface, leads to its identification as a 'true' oyster.

Ecology. Cemented epifaunal suspension-feeder.

Suborder MONOTIDINA Waterhouse, 2001 (*sensu* Wasmer *et al.* 2012)

Superfamily MONOTOIDEA Fischer, 1887 in Fischer 1880–1887

Family MONOTIDAE Fischer, 1887 in Fischer 1880–1887

Genus UNCERTAIN

Monotidae indet.

Figures 6O–P

Material. One incompletely preserved internal mould of a LV.

Description. Shell medium sized, elliptical, longer than high, moderately inflated, inequilateral, retrocrescent; beak acute, slightly prosogyrate, slightly projecting above straight and relatively short dorsal margin; anterior and posterior wing weakly demarcated from disc; irregular and uneven radial ribs, increasing in number by intercalation, first order ribs starting close to beak, at the posterior part of the shell hardly distinguishable from second order ribs, second order ribs starting approximately in the middle part of the shell, generally narrow interspaces between ribs, interspaces on postero-dorsal part of shell are narrowest.

Remarks. *Monotis* is an index fossil for the middle Norian to early Rhaetian (McRoberts *et al.* 2008) and likely arose from *Meleagrinella* Whitfield, 1885 during the early or middle Norian (McRoberts 2010, 2017). It is therefore surprising to find a bivalve with a *Monotis*-like morphology in Anisian strata. Given the unusual stratigraphic occurrence and the incomplete preservation, it seems possible that this species represents a Middle Triassic homeomorph of *Monotis*. We therefore assign this taxon only tentatively to the Monotidae.

Ecology. For *Monotis*, the type genus of the Monotidae, several modes of life have been suggested, ranging from epibyssally attached to hard substratum (Stanley 1972; Hallam 1981; McRoberts *et al.* 2008) or plants (Grant-Mackie 1980; Ando 1987) to pseudoplanktonic (Hayami 1969; Stanley 1972; Silberling *et al.* 1997) or nektonic (Jefferies & Minton 1965). The exact mode of life of the Dobrogea specimen remains speculative.

Suborder LIMINA Waller, 1978

Superfamily LIMOIDEA Rafinesque, 1815

Family LIMIDAE Rafinesque, 1815

Genus MYSIDIOPTERA Salomon, 1895

Type species. *Mysidioptera ornata* Salomon, 1895.

Mysidioptera fornicata Bittner, 1895

Figures 6E–G

*1895 *Mysidioptera fornicata*; Bittner, p. 184, pl. 20, fig. 11.

2004 *Mysidioptera fornicata* Bittner; Komatsu *et al.*, fig. 7(2).

Material. 13 LVs, 15 RVs and two unassigned valves, one of them showing the shell's interior.

Description. Shell medium sized, moderately to strongly inflated, equivalve, inequilateral, slightly procrescent, suborbicular to obliquely ovate in outline, height/length-ratio variable, either higher than long or vice versa; beak obtuse, prosogyrate; anterior margin concave, lunula deeply impressed, with byssal gape between valves, postero-dorsal margin straight; anterior auricle absent, posterior auricle obtuse, not well demarcated from main body of shell; externally smooth except for slightly irregular growth lines on disc and posterior auricle, occasionally fine radial ribs present on disc, hardly recognizable on umbonal region, lunula with strong growth lines.

Remarks. Nearly 100 *Mysidioptera* species have been reported from the Triassic and several of these are smooth or weakly ornamented (Posenato 2008). *Mysidioptera* species that are weakly ornamented with radial elements and strongly inflated include *M. fornicata* Bittner, 1895, *M. globosa* Broili, 1903, *M. inflata* Wilckens, 1909, *M. kittlii* Bittner, 1895 and *M. tommasii* Sacchi Vialli & Vai, 1958. The Dobrogea specimens show most similarities with *M. fornicata*, which is characterized by a suborbicular outline, a higher than long shell, a straight postero-dorsal margin and the presence of radial striae on the lunula and in the umbonal region. According to Broili (1903), *M. globosa* has densely spaced, weak radial ribs that undulate where intersecting strong growth lines, a feature that is not present in the Dobrogea specimens. *M. kittlii* and *M. inflata* have the same ornamentation as

M. *globosa* and Wilckens (1909) assigned these three species to the subgenus *Latemaria*, because of their strong inflation. Furthermore, *M. kittlii* does not possess a lunula or a byssal gape (Bittner 1895). The beak of *M. tommasii* described by Speciale (1967) is acute and the inflation of the disc decreases towards the shell margin, which is not the case in the Dobrogea specimens.

Ecology. The equivalved condition and the presence of a byssal notch suggest that specimens of *M. fornicata* rested orthothetically and byssally attached on the sediment.

Occurrence. Leidapo Member (China, late Pelsonian – early Illyrian; Komatsu *et al.* 2004), Cassian Formation (Italy, Longobardian–Julian; Bittner 1895).

Mysidioptera sp.

Figures 6L

Material. One articulated specimen and possibly one additional LV.

Description. Shell medium sized, moderately inflated, procrescent, equivalve, inequilateral, subtrigonal, higher than long; beak orthogyrate, acute, slightly projecting above probably straight dorsal margin; anterior margin concave; anterior auricles not preserved, posterior auricle small, obtuse, well demarcated from body shell; shell smooth except for fine and regular growth lines on body shell.

Remarks. The overall morphology indicates that these specimens belong to the genus *Mysidioptera*. However, none of the smooth *Mysidioptera* species reported from the Triassic possesses a posterior auricle that is as well demarcated from the body shell as that of these specimens. Because of the limited material and incomplete preservation, we describe these specimens in open nomenclature rather than establishing a new species.

Ecology. Same as for *Mysidioptera fornicata*.

Genus PLAGIOSTOMA J. Sowerby, 1814

Type species. *Plagiostoma gigantea* J. Sowerby, 1814.

Plagiostoma striatum (von Schlotheim, 1820)

Figures 6H–J

*1820 *Chamites striatus*; von Schlotheim, p. 210.

1823 *Chamites striatus* von Schlotheim; Schlotheim, pl. 34, fig. 1.

1923 *Lima* (*Plagiostoma*) *striata* (von Schlotheim); Diener, p. 107 [cum syn.].

1928 *Lima striata* (von Schlotheim); Schmidt, p. 154, fig. 326.

1937 *Lima striata* (von Schlotheim); Assmann, p. 49, pl. 10, fig. 14.

1967 *Plagiostoma striatum* (von Schlotheim); Speciale, p. 1109, pl. 82, fig. 7 [cum syn.].

2003 *Plagiostoma striatum* (von Schlotheim); Szente & Vörös, p. 128, pl. 2, fig. 2 [cum syn.].

2004 *Plagiostoma striatum* (von Schlotheim); Komatsu *et al.*, fig. 7(18).

2008 *Plagiostoma striatum* (von Schlotheim); Posenato, p. 101, fig. 3O [cum syn.].

2015 *Plagiostoma striatum* (von Schlotheim); Hagdorn, fig. 7.11.

2016 *Plagiostoma striatum* (von Schlotheim); Brom *et al.*, fig 1E.

2017 *Plagiostoma striatum* (von Schlotheim); Foster & Sebe, p. 168, fig. 3M.

Material. 49 LVs, 30 RVs and nine unassigned shell fragments.

Description. Shell medium sized, ovate, higher than long, procrescent, equivalve, inequilateral, moderately inflated; beak prosogyrate, obtuse; dorsal margin angulated, antero-dorsal margin shorter than postero-dorsal one, anterior margin mostly straight, occasionally slightly concave; auricles obtuse and faintly demarcated from flank, anterior auricles smaller than posterior ones, small byssal gape between valves below anterior auricle; lunula large, elongated, impressed, located dorsally to anterior umbonal ridge and comprising nearly the entire antero-dorsal margin (Fig. 6I); up to 60 radial ribs that start close to beak, crests flattened but getting rounded towards ventral margin, very narrow and punctate interspaces getting broader towards ventral margin where they are almost as broad as the ribs, number of ribs increasing by bifurcation, occasionally ribs and interspaces getting broader distally but sometimes also remaining relatively narrow, occasionally ribs curved on ventral parts of shell, auricles bearing ribs and occasionally weak growth lines, growth lines strong on lunula and anterior auricles.

Remarks. This well-known Middle Triassic species is very abundant in the samples from Dobrogea. Our material agrees very well with specimens from the type area in the Germanic Basin, although some specimens have a slightly higher number of ribs (up to 60) than typical specimens from the Muschelkalk (30–50; Schmidt 1928).

Ecology. Species of the genus *Plagiostoma* are interpreted as epibyssate suspension-feeders (Seilacher 1954; McRoberts 2017).

Occurrence. Gogolin Beds (Poland, late Olenekian – early Pelsonian; Brom *et al.* 2016), Jena Formation (Germany, late Bithynian – early Illyrian; Wagner 1897; Assmann 1937; Schmidt 1928, 1938; Klotz & Lukas 1988), Valle Trompia (Italy, middle Anisian; Speciale 1967), Felsőörs Formation (Hungary, Pelsonian–Illyrian; Szente & Vörös 2003), Zuhánya Limestone (Hungary, late Pelsonian – early Illyrian; Foster & Sebe 2017), Leidapo Member (China, late Pelsonian – early Illyrian; Stiller 2001; Komatsu *et al.* 2004), Karlstadt Formation, Heilbronn Formation, Diemel Formation (Germany, early Illyrian; Assmann 1937; Schmidt 1928, 1938), Trochitenkalk Formation (Germany, middle Illyrian; Wagner 1897; Schmidt 1928, 1938; Busse 1972; Hagdorn & Ockert 1993; Ockert 1993), Meissner Formation (Germany, late Illyrian – early Longobardian; Wagner 1897; Schmidt 1928, 1938; Busse 1972; Hagdorn & Mundlos 1982; Hagdorn & Ockert 1993), Dont Formation (Italy, Pelsonian–Illyrian; Posenato 2008), Erfurt Formation (Germany, early Longobardian; Schmidt 1928, 1938; Hagdorn 2015).

Plagiostoma cf. *angulatum* (Münster, 1841)

Figures 6M–N

cf. *1841 *Lima angulata*; Münster, p. 73, pl. 6, fig. 30.

cf. 1895 *Lima angulata* Münster; Bittner, p. 173, pl. 22, figs 3–5.

cf. 1903 *Lima angulata* Münster; Broili, p. 176, pl. 20, figs 1–3, 10.

cf. 1909 *Lima angulata* Münster; Wilckens, p. 132, pl. 5, fig. 15.

cf. 1923 *Lima angulata* Münster; Diener, p. 102 [cum syn.].

cf. 1981 *Plagiostoma angulata* [*sic*] (Münster); Zardini, pl. 17, fig. 24.

Material. One LV and two RVs, one of them an internal mould with some shell remains.

Description. Shell medium sized, inequilateral, obliquely ovate in outline with the axis of greatest elongation oriented from postero-dorsal to antero-ventral, higher than long, procrescent, moderately inflated; beak slightly prosogyrate, acute, slightly projecting above short hinge margin; anterior shell margin straight; lunula triangular, elongated, located dorsally of anterior umbonal ridge; auricles small, obtuse and faintly demarcated from flank, anterior auricle smaller than posterior one; radial ribs with rounded crests that start close to beak, up to 25 first order ribs getting broader ventrally, also visible on internal mould, interspaces between first order ribs variable in width, covered with several (up to three) fine radial ribs that are not visible on internal moulds, posterior auricle with radial ribs, anterior auricle with well-developed incremental lines.

Remarks. The Dobrogea specimens are morphologically similar to *Lima angulata* Münster, 1841. However, Bittner (1895) mentioned that the higher order ribs in this species vary in thickness and few can become as broad as the first order ribs. Furthermore, higher order ribs can be located on the

flanks of first order ribs in larger specimens with thin first order ribs. Both features were not observed in the Dobrogea specimens. Bitter (1895) further mentioned that higher order ribs are more abundant on the posterior part. In the Dobrogea specimens such a dominance of higher order ribs in the posterior part of the shell is not observable. Although Bittner (1895) pointed out that irregularities concerning the number, strength and distribution of ribs are a conspicuous feature of this species, we prefer to retain this species in open nomenclature.

Ecology. Same as for *Plagiostoma striatum*.

Occurrence. Cima Viezzena (Italy, Longobardian; Wilckens 1909), Pachycardientuffe (Italy, late Longobardian; Broili 1903; Blaschke 1905; Waagen 1907), Cassian Formation (Italy, Longobardian–Julian; Bittner 1895; Pia 1937; Zardini 1981).

Subclass PALAEOHETERODONTA Newell, 1965

Order TRIGONIIDA Dall, 1889

Superfamily MYOPHORIOIDEA Bronn, 1849 in Bronn 1848–1849

Family MYOPHORIIDAE Bronn, 1849 in Bronn 1848–1849

Genus ELEGANTINIA Waagen, 1907

Type species. *Lyrodon elegans* Dunker, 1851.

Remarks. The classification of *Elegantinia* and the closely related genus *Gruenewaldia* within Myophoriidae, Gruenewaldiidae or Trigoniidae has been debated (e.g. Newell & Boyd 1975, 1987; Cooper 1991; Boyd & Newell 1997). Based on hinge morphology and the absence of trigonioid pedal muscles, Hautmann (2003) suggested retaining these genera within Myophoriidae, which is followed herein.

Elegantinia elegans (Dunker, 1849)

Figures 7A–B

*1849 *Lyriodon elegans*; Dunker, p. 15.

1928 *Myophoria elegans* (Dunker); Schmidt, p. 193, fig. 455.

1975 *Lyriomyophoria elegans* (Dunker); Newell & Boyd, p. 148, fig. 89.

1976 *Myophoria* (*Elegantinia*) *elegans* (Dunker); Gu *et al.*, pl. 21, figs 1–9.

2004 *Elegantinia elegans* (Dunker); Komatsu *et al.*, p. 216, figs 12–13.

2015 *Elegantinia elegans* (Dunker); Hagdorn, p. 120, fig. 7.20.

Material. One almost complete RV.

Description. Shell medium sized, longer than high, subtrigonal, inequilateral, moderately inflated, anterior and ventral margin rounded, posterior margin truncated; beak not preserved; marginal carina prominent, passing from umbo to postero-ventral margin, becoming broader distally; antecarinal depression present; radial groove on corselet; at least 21 strong, commarginal ribs on

flank, getting narrower toward ventral margin, interspaces almost as broad as ribs, corselet with one radial rib behind radial groove, more and finer commarginal ribs than on flank, no ornamentation visible on marginal carina and antecarinal depression; hinge with two smooth teeth, merged below the beak (Fig. 7B).

Remarks. The Dobrogea specimen agrees in all observed characters with the morphology of *Elegantinia elegans*, a species that is widespread in the Muschelkalk of the Germanic Basin but also reported from the Anisian of China.

Ecology. Shallow infaunal suspension-feeder.

Occurrence. Phra That Fm. (Thailand, Lower Triassic; Vu Khuc 2000), Röt Formation (Germany, early Bithynian; Schmidt 1928, 1938), Jena Formation (Germany, late Bithynian – early Illyrian; Wagner 1897; Schmidt 1928, 1938), Leidapo Member (China, late Pelsonian – early Illyrian; Gu *et al.* 1976; Stiller 2001; Komatsu *et al.* 2004), Karlstadt Formation, Heilbronn Formation, Diemel Formation (Germany, early Illyrian; Schmidt 1928, 1938), Trochitenkalk Formation (Germany, middle Illyrian; Wagner 1897; Schmidt 1928, 1938; Busse 1972; Hagdorn & Ockert 1993; Ockert 1993), Meissner Formation (Germany, late Illyrian – early Longobardian; Wagner 1897; Schmidt 1928, 1938; Hagdorn & Ockert 1993; Ockert 1993), Erfurt Formation (Germany, early Longobardian; Schmidt 1928, 1938; Hagdorn 2015).

Genus HEMINAJAS Neumayr, 1891

Type species. *Myophoria fissidentata* von Wöhrmann, 1889.

Remarks. We follow Hautmann *et al.* (2013) and place *Heminajas*, which has three teeth in its RV, within the Myophoriidae, in which a relatively weak third tooth may be present in their RVs, and not in the Trigonodidae (= Pachycardiidae in Cox *et al.* 1969), which do not possess more than two teeth in each of their valves (Cox *et al.* 1969).

Heminajas? sp.

Figure 7C

Material. One almost completely preserved RV.

Description. Shell medium sized, elliptical, longer than high, inequilateral, retrocrescent; beak positioned in anterior part of shell, projecting dorsal margin; slight depression in front of the umbo creating a flattening of the shell towards the anterior margin; regular growth lines, regular radial lines best visible at anterior and posterior part of the shell, growth lines and radial lines create a weak reticular pattern.

Remarks. The morphology of the Dobrogea specimen is similar to that of *Heminajas*. However, neither a weak umbonal carina nor the truncated posterior margin are present/preserved in the Dobrogea specimen. Furthermore, the internal characters are not observable, which makes the generic assignment uncertain. The radial lines may result from the shell microstructure.

Ecology. Shallow infaunal suspension-feeder.

Order MODIOMORPHOIDA Cox *et al.,* 1969

Superfamily MODIOMORPHOIDEA Miller, 1877

Family HEALEYIDAE Hautmann, 2008

Genus JOANNINA Waagen, 1906

Type species. *Joannina joannae* Waagen, 1906.

Remarks. We follow Hautmann (2008) and place *Joannina* within Healeyidae and this family within Modiomorphoidea.

Joannina aff. *joannae* Waagen, 1906

Figure 7D

aff. *1906 *Joannina joannae*; Waagen, p. 390.

aff. 1907 *Joannina joannae* Waagen; Waagen, p. 34, pl. 34, figs 12–14.

Material. One RV.

Description. Shell medium sized, subrectangular-modioliform, retrocrescent; beak subterminal and prosogyrate, giving rise to pronounced diagonal ridge; diagonal ridge sharp near beak, becoming flatter and broader towards postero-ventral margin, separating flank from posterior area; median depression on center of flank separating anterior shell lobe; posterior area with blunt, faint radial structure but no distinct ridges; ornamentation with several pronounced growth irregularities and fine incremental lines becoming irregular to weavy on posterior area.

Remarks. This species is similar to *Joannina joannae* Waagen, 1906 from the late Ladinian, but it differs in being more rectangular in outline and lacking two sharp ridges on the posterior area (see Hautmann 2008 for a description of *J. joannae*). These differences are probably sufficient for distinguishing this taxon as a new species, but with the limited material available to us, we provisionally describe it in open nomenclature.

Ecology. Hautmann (2008) suggested an endobyssate mode of life for *Joannina* because of its modioliform shell and the presence of a byssal gape.

Family KALENTERIDAE Marwick, 1953

Genus MYOCONCHA J. Sowerby, 1824

Type species. *Myoconcha crassa* J. Sowerby, 1824.

Remarks. The 'actinodont' hinge of the Kalenteridae indicates their affiliation to the Modiomorphoidea and Palaeoheterodonta (Hautmann 2001*a*). In contrast, Kaim & Schneider (2012) placed the Kalenteridae in the Carditida within Heteroconcha, because the inner shell layer of *Myoconcha* and *Caspiconcha* is cross-lamellar, rather than nacreous. However, the crossed-lamellar shell structure developed several times independently, e.g. in Pectinida and Heterodonta (e.g. Carter 1990). We therefore regard the hinge morphology as a more important taxonomic character than the shell structure.

Myoconcha sp.

Figure 7E

Material. One posterior fragment of a RV.

Description. Medium sized fragment of posterior part of shell externally covered by at least 12 narrow radial ribs and straight, sub-commarginal rib-like growth lines, forming tubercules where intersecting radial ribs.

Remarks. The shape and ornamentation of the studied fragment are indicative of *Myoconcha*. The sculpture and number of ribs of the described specimen show most similarities with *Myoconcha appeli* Kittl, 1903, *Myoconcha maximiliani-leuchtenbergensis* von Klipstein, 1843 and *Myoconcha pavida* Bittner, 1901, but incomplete preservation prevents us from a firm assignment.

Ecology. Hodges (2000) suggested an endobyssate mode of life for oval-modioliform specimens of *Myoconcha*, whereas Kaim & Schneider (2012) suggested an epifaunal mode of life for mytiliform *Myoconcha* specimens. Because of its incomplete preservation the exact mode of life for the Dobrogea specimen remains unclear.

Subclass HETERODONTA Neumayr, 1884

Infraclass EUHETERODONTA Giribet & Distel, 2003

Order LUCINIDA Gray, 1854

Superfamily LUCINOIDEA Fleming, 1828

Family MACTROMYIDAE Cox, 1929

Genus UNICARDIUM d'Orbigny, 1849

Type species. *Corbula cardioides* Phillips, 1829.

Unicardium schmidii (Geinitz, 1842)

Figures 7F–H

*1842 *Arca*? *schmidii*; Geinitz, p. 557, pl. 10, fig. 9.

1859 *Arca*? *schmidii* Geinitz; von Schauroth, p. 323, pl. 2, fig. 16.

1923 *Unicardium schmidi* (Geinitz); Diener, p. 121 [cum syn.].

1928 *Unicardium schmidi* (Geinitz); Schmidt, p. 199, fig. 476.

Material. Six LVs, three RVs and three additional specimens, mostly incompletely preserved. Two of them are preserved as internal moulds.

Description. Shell medium sized, elliptical, equivalve, slightly inequilateral, moderately inflated; beak strongly prosogyrate, obtuse, located almost in the middle of straight dorsal margin and distinctly projecting above it; ligament parivincular, nymph long and straight (Fig. 7G); hinge edentulous; postero-dorsal margin slightly higher than antero-dorsal margin; strong commarginal ribs with interspaces becoming narrower towards ventral margin, growth lines visible in interspaces.

Remarks. The Dobrogea specimens agree very well with *Unicardium schmidii*, as described in Schmidt (1928), including the edentulous hinge. However, *Unicardium* d'Orbigny, 1849 was originally described as having a tooth in its hinge (d'Orbigny 1849, p. 218), and the question arises whether the edentulous *U. schmidii* really belongs to this genus or, more generally, whether the presence or absence of a hinge tooth is within the variability of the genus. Unfortunately, the hinge of the type species of *Unicardium*, *Corbula cardioides* Phillips, 1829, was neither described nor illustrated so far. Stoliczka (1871, p. 246) noted that *Unicardium* has a hinge with one cardinal tooth in each valve that is occasionally obsolete or nearly so, which seems to justify the assignment of *U. schmidii* to this genus.

Ecology. Moderately deep infaunal suspension-feeder.

Occurrence. Röt Formation (Germany, early Bithynian; Schmidt 1928, 1938), Jena Formation (Germany, late Bithynian – early Illyrian; Wagner 1897; Schmidt 1928, 1938; Klotz & Lukas 1988), Trochitenkalk Formation (Germany, middle Illyrian; Wagner 1897; Schmidt 1928, 1938; Ockert 1993), Meissner Formation (Germany, late Illyrian – early Longobardian; Wagner 1897; Schmidt 1928, 1938; Busse 1972; Hagdorn und Ockert 1993), Erfurt Formation (Germany, early Longobardian; Schmidt 1928, 1938).

Family LUCINIDAE Fleming, 1828

Genus SCHAFHAEUTLIA Cossmann, 1897

Type species. *Gonodon schafhaeutli* Salomon, 1895.

Remarks. We follow the conventional assignment of *Schafhaeutlia* to the Lucinidae (e.g. Cox *et al.* 1969), but we note that the morphological evidence for this is questionable.

Schafhaeutlia astartiformis (Münster, 1841)

Figures 7I–K

*1841 *Isocardia astartiformis*; Münster, p. 87, pl. 8, fig. 24.

1865 *Corbis astartiformis* (Münster); Laube, p. 37, pl. 15, fig. 5.

1895 *Gonodon astartiformis* (Münster); Bittner, p. 12, pl. 3, figs 1–4.

1903 *Gonodon astartiformis* (Münster); Broili, p. 218, pl. 27, figs 30–31.

1909 *Schafhäutlia astartiformis* (Münster); Wilckens, p. 162, pl. 6, fig. 11.

1923 *Schafhäutlia astartiformis* (Münster); Diener, p. 217 [cum syn.].

1966 *Gonodon astartiformis* (Münster); Allasinaz, p. 701, pl. 54, figs 6–7.

1981 *Schafhaeutlia astartiformis* (Münster); Zardini, pl. 33, figs 8a–b; pl. 34, figs 1–6.

Material. Four LVs, one RV and one articulated specimen. Mostly incompletely preserved or internal moulds.

Description. Shell medium sized, moderately inflated, slightly inequilateral, elliptical, longer than high; beak strongly prosogyrate, obtuse, located close to the middle of dorsal margin and clearly projecting above it; nymph long and straight; ligament parivincular; cardinal tooth 3a observed in one specimen (Fig. 7J); irregular growth lines variable in strength, occasionally forming weak ribs.

Remarks. The overall shape in combination with the morphology of cardinal tooth 3a (Fig. 7J) is indicative of *Schafhaeutlia*. However, already Bittner (1901) noted that species of this genus are difficult to distinguish from each other. We found the best agreement with *Schafhaeutlia astartiformis*, a well-known species that occurs in many Middle and Late Triassic localities.

Ecology. Hautmann (2001*a*) proposed an epibenthic mode of life for *Schafhaeutlia sphaerioides*. According to Hautmann (2001*a*), *S. sphaerioides* rested on its flattened anterior side with the strongly curved beaks stabilizing this position. However, the anterior margin of *S. astartiformis* is well rounded and not flattened, suggesting a shallow infaunal mode of life.

Occurrence. Leidapo Member (China, late Pelsonian – early Illyrian; Stiller 2001; Komatsu *et al.* 2004), Cima Viezzena (Italy, Longobardian; Wilckens 1909), Pachycardientuffe (Italy, late Longobardian; Broili 1903; Blaschke 1905), Cassian Formation (Italy, Longobardian–Julian; Laube 1865; Bittner 1895; Fürsich & Wendt 1977; Zardini 1981), Sella delle Cave (Italy, Julian; Allasinaz 1966).

Schafhaeutlia? *trigona* (Stoppani, 1858)

Figure 7L

*1858 *Cyprina trigona*; Stoppani, p. 85, pl. 17, fig. 8.

Material. Two LVs.

Description. Shell small to medium sized, elliptical, longer than high, slightly inflated, inequilateral; beak strongly prosogyrate, obtuse, clearly projecting above straight dorsal margin, positioned at the anterior part of the shell; fine, regular growth lines well visible with naked eye.

Remarks. The main features of the Dobrogea specimens are in accordance with the main characteristics of *Cyprina trigona*. Rossi Ronchetti (1959) assigned a morphologically similar species to *Schafhaeutlia*. Although the Dobrogea specimens, as well as the specimens illustrated in Stoppani (1858) and Rossi Ronchetti (1959), resemble the shape of *Schafhaeutlia*, the anteriorly positioned beak is unusual for this genus. Unfortunately, the internal characters of the Dobrogea specimens are

not observable, which makes an assignment at the genus level uncertain. This species differs from *Schafhaeutlia astartiformis* by its shape and the fine and regular growth lines.

Ecology. Same as for *Schafhaeutlia astartiformis*.

Occurrence. Esino Limestone (Italy, Ladinian; Stoppani 1858).

Order MEGALODONTIDA Starobogatov, 1992

Superfamily MEGALODONTOIDEA Morris & Lycett, 1853

Family DICEROCARDIIDAE Kutassy, 1934?

Genus PRAEDICEROCARDIUM n. gen.

LSID. urn:lsid:zoobank.org:act:A36FA7B2-1F30-497E-B56C-C791F54E1873

Derivation of name. Combination of *prae* (Latin: before) and the genus name *Dicerocardium*.

Type species. *Praedicerocardium vetulus* n. gen. et n. sp.

Diagnosis. Shell equivalve; valves triangular; flank delimited anteriorly and posteriorly by sharp ridges converging towards the umbo; angle included between ridges acute; shell region in front of anterior

ridge flattened; shallow but broad radial shell depressions in front of posterior ridge and narrow escutcheon behind it; beaks terminal; umbones strongly prosogyrate but not elevated above flat anterior shell region.

Remarks: Because the hinge structure is not observable, the external shell morphology is the sole basis for a discussion about the taxonomic position of the genus. The new genus closely resembles species assigned to *Dicerocardium* Stoppani, 1865 (e.g. *Dicerocardium dolomiticum marianii* Frech, 1904) in terms of its triangular shape, flattened anterior shell region and the presence of an anterior and posterior carina. However, it differs from *Dicerocardium* by the morphology of the umbones, which are less incoiled and not elevated above the flat anterior shell region. Moreover, the stratigraphical occurrences differ considerably: *Dicerocardium* is Norian (Végh-Neubrandt 1982), thus appearing about 20 million years later than *Praedicerocardium*.

Based on the similarity in the external morphology, we place the new genus tentatively in Dicerocardiidae, rather than in Megalodontidae. If correct, the new genus predates considerably the oldest stratigraphic appearance of the Dicerocardiidae from the Carnian (Végh-Neubrandt 1982, Tab. 18) to the Anisian. Moreover, it also predates the stratigraphical oldest Triassic megalodontid, which is a (questionable) report from the Meissner Formation ('*Megalodon securiformis*' Schmidt, 1928) that is late Illyrian (late Anisian) to early Longobardian (late Ladinian) in age (Hagdorn & Nitsch 2009). If Dicerocardiidae evolved from Megalodontidae (Cox *et al.* 1969; Végh-Neubrandt 1982), the early stratigraphic appearance of Dicerocardiidae in the Middle Triassic implies a considerable outage in the fossil record of Megalodontidae during the Early and early Middle Triassic.

The new genus has also implications for the phylogeny of Dicerocardiidae. Végh-Neubrandt (1982, p. 116–117) suggested that *Dicerocardium* derives from a carnian lineage that led from *Laubeia* via *Physocardia* and *Cornucardia* to the Norian *Dicerocardium*. We suggest that *Praedicerocardium* is another candidate ancestor, which is in its external morphology much closer to *Dicerocardium* than is

Physocardia. Future data on the hinge structure may help to decide whether this similarity in the external morphology resulted from phylogenetic relationships of convergent evolution.

Praedicerocardium vetulus n. gen. et n. sp.

Figures 7M–P

LSID. urn:lsid:zoobank.org:act:F1CC713D-556D-4971-AA99-B0253CA28F79

Derivation of name. *Vetulus* (Latin: old), because it is the geologically oldest Triassic megalodontoid.

Holotype. LPB IIIL 2142

Paratypes. LPB IIIL 2143, IIIL 2144

Material. One LV, two RVs and one articulated specimen.

Diagnosis: Same as for the genus.

Description. Shell large, trigonal, longer than high, highly inequilateral, strongly inflated; shell thick, consisting of two shell layers, the outer layer approximately 1 mm thick, the inner layer approximately 3–4 mm thick; beaks strongly coiled, prosogyrate, terminal, clearly projecting above dorsal margin; anterior part of shell flat, separated from flank by sharp ridge extending from umbo to

antero-ventral margin; escutcheon narrow, separated from flank by sharp escutcheon ridge, shallow but broad radial shell depression anterior to escutcheon ridge; anterior margin straight, posterior margin slightly curved, distally almost straight; regular growth lines, fine and slightly irregular commarginal ribs present in one specimen; internal structures not observed.

Ecology. According to Zapfe (1957) and Végh-Neubrandt (1982), equivalved megalodontids were semi-infaunal or epifaunal suspension-feeders that rested on their anterior shell margin and beaks. In this position, the flat and relatively large anterior part of *Praedicerocardium vetulus* provided a resting surface and prevented the animal from sinking into the soft sediment. Alternatively, *Praedicerocardium vetulus* might have rested on the straight postero-dorsal margin, as suggested by Schneider (2017) for the Jurassic *Pachyrisma*. This position would also be stable, supported by the escutcheon ridges and the center of gravity of the shell. Furthermore, it would expose the respiratory margin directly into the free water column. However, it raises the problem how the animal could adopt this position, given that its foot would also be directed towards the free water column, without contact to the sediment and therefore essentially inoperable.

Order ANOMALODESMATA Dall, 1889

Suborder PHOLADOMYIDA Newell, 1965

Superfamily PHOLADOMYOIDEA King, 1844

Family MEGADESMIDAE Vokes, 1967

Genus ROMANIAMYA n. gen.

LSID. urn:lsid:zoobank.org:act:5CAB38FD-6B23-43C0-A750-2C2E55F501AD

Derivation of name. Combination of 'Romania' and the genus name *Mya*.

Type species. *Romaniamya mahmudiaensis* n. gen. et n. sp.

Diagnosis. Putative megadesmid bivalves with shell slightly expanding posteriorly, having a shallow median depression on the flank, a moderate siphonal gape, a straight dorsal margin with short anterior and posterior projections and a blunt posterior umbonal ridge.

Remarks. This enigmatic taxon shows some similarities with late Palaeozoic anomalodesmats that are usually referred to the family Megadesmidae (e.g. Cox *et al.* 1969; Runnegar 1974), most notably with the Permian *Pachymyonia* Dun, 1932. Some of these megadesmids possess a well-developed umbonal ridge, short distal projections of the nearly straight dorsal margin, a shallow depression on the flank and a siphonal gape, but a combination of these characters as in the Dobrogea specimens is unknown so far.

Romaniamya mahmudiaensis n. gen. et n. sp.

Figures 8A–B

LSID. urn:lsid:zoobank.org:act:4E73DC0A-5A9D-4D76-9943-3339A2A49CB7

Derivation of name. Referring to the type locality near Mahmudia, North Dobrogea, Romania.

Holotype. LPB IIIL 2145

Paratype. LPB IIIL 2146

Material. One LV and internal moulds of an articulated specimen and a LV.

Diagnosis. Same as for the genus.

Description. Shell medium sized, elongated, trapeziform, inequilateral, equivalve, moderately inflated; very shallow median depression on centre of flank; beaks slightly prosogyrate, obtuse, positioned in front of the midline of straight dorsal margin and slightly projecting above it; umbonal ridge prominent, broad, starting close to beak and running towards the postero-ventral part of the shell; sulcus located dorsally to umbonal ridge (Fig. 8B); postero-dorsal margin straight, ventral margin almost straight; slightly gaping at posterior end (Fig. 8B); irregular and weak commarginal ribs present; internal structures unknown.

Remarks. *Macrodon taramellii* Parona, 1889 is very similar to *Romaniamya mahmudiaensis* but it differs from *R. mahmudiaensis* by the shape of the antero-dorsal margin and the presence of fine radial striae. Parona (1889) noted that the ligament area was not observable in his specimens, therefore his assignment to *Macrodon* is uncertain.

Ecology. The posterior gape suggests the presence of well-developed siphons and therefore a deep-infaunal mode of life.

Superfamily UNCERTAIN

Family UNCERTAIN

Genus UNCERTAIN

Anomalodesmata indet. A

Figure 8C

Material. One incompletely and poorly preserved internal mould of a RV.

Description. Shell medium sized, elongated, slightly inflated, strongly inequilateral, retrocrescent; beak close to anterior margin, slightly projecting long dorsal margin; dorsal and ventral margin subparallel to each other.

Remarks. The shape of this internal mould suggests an affiliation to the Anomalodesmata, but it is too incompletely preserved for a more precise determination.

Ecology. Deep infaunal suspension-feeder.

Anomalodesmata indet. B

Figure 8D

Material. One fragmented internal mould, possibly representing the posterior part of a RV.

Description. Fragment medium sized, elongated, slightly inflated, becoming broader towards posterior margin; irregular commarginal folds best visible at the margin.

Remarks. In spite of its poor and incomplete preservation, the shape of this fragment is suggestive for an anomalodesmatid. The preservation state of this specimen does not allow a more accurate assignment.

Ecology. Deep infaunal suspension-feeder.

Anomalodesmata indet. C

Figure 8E

Material. One incompletely preserved internal mould of a LV.

Description. Shell medium sized to large, elongated, moderately inflated, strongly inequilateral, retrocrescent; umbonal region curved; beak broad, ophistogyrate, slightly projecting above very long

and straight dorsal margin, positioned in anterior part of shell; ventral margin slightly concave, posterior margin straight; umbonal ridge passing from umbo towards postero-ventral edge.

Remarks. The general shape suggests an assignment to the Anomalodesmata but the incomplete preservation state of the Dobrogea specimen does not allow a definite assignment.

Ecology. Deep infaunal suspension-feeder.

INCERTAE SEDIS

Genus MYTILICONCHA Tommasi, 1911

Type species. *Mytiliconcha orobica* Tommasi, 1911.

Remarks. There has been disagreement concerning the validity of *Mytiliconcha*. Cox (1964) proposed the name *Tommasina* as a replacement name for *Mytiliconcha* Tommasi, 1911, which he thought was preoccupied by *Mytiloconcha* Conrad, 1862. However, because the spelling of Conrad's (1862) *Mytiloconcha* differs in one letter from *Mytiliconcha*, the introduction of a replacement name by Cox (1964) was unnecessary (e.g. Vokes 1980; Stiller & Chen 2006; Ros-Franch *et al.* 2014). Waller & Stanley (2005) and Ros-Franch *et al.* (2014) regarded *Mytiliconcha* as a synonym of *Protopis*, although the hinge structure of *Mytiliconcha* is unknown. In contrast, Hautmann (2008) noted that the external features of *Mytiliconcha* and *Protopis* differ profoundly. However, other characters of *Mytiliconcha* are still unknown, making the taxonomic position of *Mytiliconcha* uncertain.

Mytiliconcha cf. *orobica* Tommasi, 1911

Figures 8F–H

cf. *1911 *Mytiliconcha orobica*; Tommasi, p. 35, pl. 3, figs 21–23.

cf. 1969 *Tommasina orobica* (Tommasi); Cox *et al.*, p. N281, fig. C22(2).

Material. Three LVs and three RVs.

Description. Shell medium sized, retrocrescent, strongly inflated; beak prosogyrate, acute, projecting above dorsal margin; carina sharp, extending from beak to postero-ventral part of the shell, vanishing distally; shell smooth except for very fine and regular growth lines and faint radial lines that are occasionally visible on some specimens.

Remarks. The specimens described above agree well in their external morphology with the type material of *Mytiliconcha orobica* Tommasi, 1911, but this species has been based on rather incomplete material, which makes any assignment tentative.

Ecology. Because of the lack of a byssal gape and the strongly inflated valves the Dobrogea specimens might have been epifaunal or semi-infaunal recliners.

Occurrence. Ghegna (Italy, Ladinian; Tommasi 1911).

DISCUSSION AND RESULTS

With a total of 51 species, the Bivalvia is the most diverse invertebrate group of the *Tubiphytes*-microbial buildup in North Dobrogea. These 51 bivalve species belong to 39 genera, 29 families, 20 superfamilies, nine orders and three subclasses, respectively (Fig. 9). Based on the presence of closed ostracod carapaces, Forel & Grădinaru (2018) concluded that the fauna is essentially preserved *in situ*. This conclusion is confirmed by the presence of several bivalve shells with conjoined valves. The quality of the preservation of the bivalve fauna is variable. Some specimens are extremely well preserved and show taxonomically significant characters in detail, whereas other species are represented by fragmentary or poorly preserved specimens only. The latter is partly due to the difficult mechanical extraction of the specimens from the hard rock, which possibly also causes a bias towards a lower bivalve richness (see below). Due to incomplete preservation or the lack of information on taxonomically important shell parts, e.g. the hinge and the ligament, 29 taxa are presented in open nomenclature (Fig. 10). On the other hand, seven species and two genera are newly described (Fig. 10). This relatively high number of new species and genera probably indicates a relatively high degree of endemism, which could be related to the unique environment provided by the *Tubiphytes*-microbial buildup.

Most genera and many of the species are already known from several other Middle Triassic localities (Fig. 11). However, only two species, i.e. *Leptochondria viezzenensis* and *Elegantinia elegans* have been reported from the Early Triassic. Six species from the *Tubiphytes*-microbial buildup are known from the Muschelkalk, 13 species from the Western Tethys and eight species from the Eastern

Tethys. Only one species (*Elegantinia elegans*) has also been reported from Northwestern Panthalassa (Hayami 1975). Five species (*Gervillaria subelegans*, *Leptochondria separata*, *Entolioides deeckei*, *Mysidioptera fornicata* and *Schafhaeutlia astartiformis*) and four genera (*Atrina, Cultriopsis, Gervillaria, Mytiliconcha*) found in the Bithynian *Tubiphytes*-Limestone Member have their oldest occurrence there (Fig. 10). However, these four genera are generally rare, which makes any statement about their first occurrences uncertain. In summary, the biogeographic character of the fauna is largely determined by the palaeogeographic distance to contemporaneous occurrences, plus an endemic component that might be related to the particular environment.

Ecologically, the bivalve assemblage is clearly dominated by *Plagiostoma striatum* (Fig. 12). Far less abundant are *Neomorphotis comta*, *Leptochondria pervulgata*, *Chlamys* (*Praechlamys*) *prima*, *Mysidioptera fornicata* and *Scythentolium anisicum*. All remaining species are relatively rare, and a total number of 25 species is only represented by one individual. Simpson's index of dominance is low (0.09) and the trophic nucleus, which is the number of species comprising 80% of the individuals of an association (Neyman 1967), contains 18 species (Fig. 12). The high evenness could indicate a heterogeneous environment, a K-selected equilibrium fauna, the effects of time-averaging or a combination of these factors. The bivalve assemblage contains shallow, moderately deep and deep infaunal, byssally attached, reclining epifaunal or partly embedded semi-infaunal as well as cementing species. However, byssal attachment, epifaunal as well as semi-infaunal, represents the most abundant mode of life, which is shown by the guild-species diversity as well as the absolute abundance of guilds (Fig. 12). The epibyssate bivalves settled on the hard substratum provided by the *Tubiphytes*-microbial buildup, where the micro-encruster framework was stabilized by large volumes of synsedimentary cements (Popa *et al.* 2014). The burrowing, semi-infaunal and free-lying bivalves indicate the presence of soft substratum, which probably filled pockets between single *Tubiphytes*-microbial buildups (Fig. 13).

Concerning the richness of bivalve assemblages, a comparison with diversities of other Early and Middle Triassic bivalve faunas shows that the assemblage from North Dobrogea is more diverse than

all Early Triassic bivalve faunas (Fig. 14 and Table 1). The rarefaction analysis suggests that the bivalve richness of the investigated *Tubiphytes*-microbial buildup is undersampled (Fig. 15). Figure 14 and Table 1 also show that a set of Middle Triassic bivalve assemblages, including the Jena Formation, the Leidapo Member, the Trochitenkalk Formation, the Meissner Formation and the Pachycardientuffe are richer than all other Middle Triassic bivalve assemblages. However, because the data used for this comparison are raw data from the literature, their interpretation is difficult. Factors like oversplitting (see also Friesenbichler *et al.* 2019), a long history of research and a large outcrop area (concerning e.g. the Germanic Triassic) or a Lagerstätten effect (e.g. in the Leidapo Member) may cause a bias towards higher diversities.

In addition to the 51 bivalves species identified in this study, 21 gastropod species (Nützel *et al.* 2018) and 12 brachiopod species (Grădinaru & Gaetani 2019) have been reported so far from this locality. These 84 benthic macroinvertebrate species flourished in an environment that was constructed by micro-encrusting organisms (Popa *et al.* 2014). Based on the presence of a highly diverse invertebrate fauna associated with this microbial buildup, Nützel *et al.* (2018) concluded that benthic faunas recovered faster from the end-Permian mass extinction than metazoan reefs, an assumption that is in accordance with the results from this study. Similarly, Friesenbichler *et al.* (2019) hypothesized that the increase in environmental diversity associated with newly arising carbonate factories contributed at least in part to the accelerated pace of recovery during the Middle Triassic. The rich Bithynian invertebrate fauna of North Dobrogea associated with one of the earliest large Triassic carbonate buildups confirms to this assumption.

CONCLUSIONS

The investigated *in situ* Bithynian (early Middle Triassic) bivalve fauna from the *Tubiphytes*-Limestone Member contains 51 species that belong to 39 genera, making bivalves the most diverse benthic macroinvertebrate group reported from this unit. However, rarefaction analysis suggests that the true number of bivalve species might be even higher. This bias might be partly related to the difficulties in the mechanical sampling of the specimens. Seven species and two genera are newly described, including the earliest Triassic representative of the Megalodontoida. The reported bivalve fauna is clearly dominated by byssally attached bivalves, which were adapted to the hard substratum provided by the *Tubiphytes*-microbial buildup. The biogeographic relationships are primarily controlled by geographic distance. This fauna is the most diverse bivalve fauna of the Bithynian in terms of taxonomic richness and clearly more diverse than all Early Triassic bivalve faunas. However, its species richness is still distinctly lower than that of the most diverse bivalve faunas from later in the Anisian and the Ladinian. We suggest that the studied fauna represents the beginning of a new recovery phase that is at least partly associated with the resurgence of organic buildups at the beginning of the Middle Triassic.

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This published work and the nomenclatural acts it contains, have been registered in ZooBank: http://zoobank.org/References/C2FC303B-A96E-4982-B9BC-977280FC42B6

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FIGURE CAPTIONS

FIG. 1. A, tectonic map of the North Dobrogea Orogen. Inset map showing the regional geological setting and the location of the North Dobrogea Orogen. *Abbreviations*: CU = Consul Unit; MU = Măcin Unit; NU = Niculițel Unit; TU = Tulcea Unit. B, geological map of the Mahmudia region. C, field photograph showing the Bithynian sediments of the Caerace Formation. The dashed line marks the boundary between the Stromatactis-Limestone Member and the overlying *Tubiphytes*-Limestone Member. Car (in circle) for scale. D, close-up view showing the position of the sample site. Modified after Grădinaru (2000), Popa *et al.* (2014), Forel & Grădinaru (2018), Nützel *et al.* (2018) and Grădinaru & Gaetani (2019).

FIG. 2. Stratigraphic column of the Mahmudia Quarry. Numbers 99–122 represent sample levels from previous works (Nützel *et al.* 2018; Grădinaru & Gaetani 2019). The star marks the sample level that yielded the bivalve specimens described herein.

FIG. 3. A–B, *Parallelodon*? sp., LPB IIIL 2001; A, LV; B, dorsal view of A showing the chevron grooves of the duplivincular ligament (arrow). C–D, *Modiolus* sp. A, LPB IIIL 2002; C, LV; D, anterior view of C. E, LV of *Modiolus* sp. B, LPB IIIL 2004. F, RV of *Bositra wengensis* (Wissmann, 1841), LPB IIIL 2008. G,

RV of *Pinna simionescui* n. sp., holotype, LPB IIIL 2006. H, LV of *Atrina multicostata* n. sp., holotype, LPB IIIL 2005. I, not oriented valve of *Pinna*? cf. *raibliana* Parona, 1889, LPB IIIL 2007. J–K, LVs of *Pteria sturi* (Bittner, 1895), LPB IIIL 2009 and LPB IIIL 2010. L, RV of *Pteria* sp. A, LPB IIIL 2013. M, RV of *Pteria* sp. B, LPB IIIL 2014. N, RV's interior of *Pteria* cf. *cassiana* (Bittner, 1895), LPB IIIL 2012. Scale bars represent 1 cm (A–D, F–N) and 0.5 cm (E).

FIG. 4. A, LV of *Cultriopsis* sp., LPB IIIL 2015. B–C, *Gervillaria subelegans* (Chen, 1976), LPB IIIL 2016; B, LV; C, umbonal region of B. D, LV of Bakevelliidae indet., LPB IIIL 2018. E–G, Aviculopectinoidea n. gen. et n. sp.; E, RV, the deep byssal notch and the sculpture of the auricles are well visible, LPB IIIL 2021; F, LV, LPB IIIL 2022; G, RV, LPB IIIL 2023. H, LV of '*Pecten*' *volaris* (Bittner, 1902), LPB IIIL 2019. I, LV of *Asoella*? sp., LPB IIIL 2038. J–K, LVs of *Amphijanira*? aff. *landrana* (Bittner, 1895), LPB IIIL 2024 and LPB IIIL 2025. L–N, *Neomorphotis comta* (Goldfuss, 1833); L and N; RVs, LPB IIIL 2028 and LPB IIIL 2029; M; LV, LPB IIIL 2027. Scale bars represent 1 cm.

FIG. 5. A–B, LVs of *Leptochondria pervulgata* (Bittner, 1902), LPB IIIL 2039 and LPB IIIL 2040. C–D, LVs of *Leptochondria separata* (Reis, 1926), LPB IIIL 2049 and LPB IIIL 2050. E, LV of *Ornithopecten* cf. *katzeri* (Bittner, 1902), LPB IIIL 2058. F–H LVs of *Leptochondria viezzenensis* (Wilckens, 1909), LPB IIIL 2053, LPB IIIL 2054 and LPB IIIL 2055. I, LV of *Ornithopecten interruptus* (Bittner, 1902), LPB IIIL 2057. J–M, *Chlamys* (*Praechlamys*) *prima* n. sp.; J and L, LVs, the auricle's sculpture is well visible, paratypes, LPB IIIL 2060 and 2061; K, LV, holotype, LPB IIIL 2062; M, external mould of a LV, paratype, LPB IIIL 2063. N, RV of *Pleuronectites*? cf. *balatonicus* (Bittner, 1901), LPB IIIL 2068. O, LV of *Avichlamys*? cf. *nicolensis* (Ogilvie Gordon, 1927), LPB IIIL 2059. P–Q, Pectinidae indet.; P, internal mould of a RV, LPB IIIL 2066; Q, internal mould of a LV, LPB IIIL 2067. R, LV of *Entolium reticulatum* n. sp. showing the shell's reticular sculpture, holotype, LPB IIIL 2070. S–U *Entolioides deeckei* (Parona, 1889). S, LV. Arrow shows the depression subparallel to posterior margin, LPB IIIL 2071. T, LV, LPB IIIL

2072; U, interior of a LV. Dotted line marks the posterior adductor muscle, LPB IIIL 2073. V, LV of *Entolium* sp., LPB IIIL 2159. Scale bars represent 1 cm (A–D, F, H–V) and 0.5 cm (E and G).

FIG. 6. A–D, *Scythentolium anisicum* n. sp.; A, RV of holotype, LPB IIIL 2075; B, LV of holotype, LPB IIIL 2075; C, RV with *Plagiostoma striatum* (LPB IIIL 2102), paratype, LPB IIIL 2076; D, fragmented RV showing the antimarginal structure (arrow), paratype, LPB IIIL 2082. E–G, RVs of *Mysidioptera fornicata* Bittner, 1895, LPB IIIL 2089, LPB IIIL 2090 and LPB IIIL 2091, the weak radial sculptural elements are best visible in E and G. H–J, *Plagiostoma striatum* (von Schlotheim, 1820); H, RV, LPB IIIL 2102; I, anterior view of a RV showing the lunula (arrow), LPB IIIL 2103; J, RV, LPB IIIL 2104. K, LV of *Umbrostrea*? sp., LPB IIIL 2087. L, LV of an articulated specimen of *Mysidioptera* sp., LPB IIIL 2101. M–N, *Plagiostoma* cf. *angulatum* (Münster, 1841); M, fragmented LV well showing the shell's sculpture, LPB IIIL 2128; N, RV, LPB IIIL 2127. O–P, Monotidae indet., LPB IIIL 2088; O, internal mould of a LV; P, dorsal view of O. Scale bars represent 1 cm.

FIG. 7. A–B, *Elegantinia elegans* (Dunker, 1849), LPB IIIL 2130; A, RV's exterior; B, interior of A showing the two merged hinge teeth (arrow). C, RV of *Heminajas*? sp., LPB IIIL 2131. D, RV of *Joannina* aff. *joannae* Waagen, 1906, LPB IIIL 2132. E, fragmented RV of *Myoconcha* sp., LPB IIIL 2133. F–H, *Unicardium schmidii* (Geinitz, 1842); F, RV, LPB IIIL 2134; G, umbonal region of H showing the nymph (arrow); H, LV, LPB IIIL 2135. I–K, *Schafhaeutlia astartiformis* (Münster, 1841); I, RV, LPB IIIL 2137; J, dorsal view of I showing parts of the hinge (arrow); K, RV, LPB IIIL 2138. L, LV of *Schafhaeutlia*? *trigona* (Stoppani, 1858), LPB IIIL 2140. M–P, *Praedicerocardium vetulus* n. gen. et n. sp.; M, dorsal view of an articulated specimen, holotype, LPB IIIL 2142; N, anterior view of a RV, paratype, LPB IIIL 2143; O, dorsal view of N; P, lateral view of N. Scale bars represent 1 cm (A, C–P) and 0.5 cm (B).

FIG. 8. A–B, *Romaniamya mahmudiaensis* n. gen. et n. sp., holotype, LPB IIIL 2145; A, LV; B, posterior view of A showing the sulcus located dorsally to the umbonal ridge (black arrow) and the shell's narrow gape (grey arrow). C, internal mould of a RV of Anomalodesmata indet. A, LPB IIIL 2148. D, not oriented specimen of Anomalodesmata indet. B, LPB IIIL 2149. E, internal mould of a LV of Anomalodesmata indet. C, LPB IIIL 2147. F–H, *Mytiliconcha* cf. *orobica* Tommasi, 1911; F, RV, LPB IIIL 2155; G, umbonal region of F; H, RV, LPB IIIL 2156. Scale bars represent 1 cm (A, C–H) and 0.5 cm (B).

FIG. 9. Pie chart showing the percentage of bivalve genera (innermost circle), families (second innermost circle), superfamilies (third innermost circle), suborders (middle circle), orders (third outermost circle), infraclasses (second outermost circle) and subclasses (outermost circle). *Abbreviations for subclasses:* i.s. = *incertae sedis*. *Abbreviations for orders:* Ar = Arcoida; Me = Megalodontida; Modiom = Modiomorphoida; Trigonii = Trigoniida; ? = uncertain. *Abbreviations for suborders:* Mo = Monotidina; Os = Ostreina; ? = uncertain. *Abbreviations for superfamilies:* Ar = Arcoidea; K = Kalenteroidea; M = Modiomorphoidea; Me = Megalodontoidea; Mo = Monotoidea; My = Myophorioidea; Mytiloi = Mytiloidea; Os = Ostreoidea; Ph = Pholadomyoidea; Po = Posidonioidea; ? = uncertain. *Abbreviations for families:* An = Antijaniridae; Bakevelli = Bakevelliidae; Di = Dicerocardiidae; H = Healeyidae; He = Heteropectinidae; Ka = Kalenteridae; Lucini = Lucinidae; Ma = Mactromyidae; Me = Megadesmidae; Mo = Monotidae; Myo = Myophoriidae; Mytili = Mytilidae; Ornitho = Ornithopectinidae; Os = Ostreidae; Pa = Parallelodontidae; Pl = Pleuronectitidae; Po = Posidoniidae; ? = uncertain. *Abbreviations for genera:* ? = uncertain.

FIG. 10. Pie chart showing the percentage of species (left circle) and genera (right circle) that (i) are newly described, (ii) the oldest and (iii) the youngest occurrence of the taxon, (iv) presented in open nomenclature, (v) species uncertainly belonging to a genus that is confirmed through the presence of another species and (vi) species and genera that do not belong to any of the just mentioned

categories. The numbers within the circular segments represent the number of species belonging to the corresponding category.

FIG. 11. Pie chart showing the percentage of species occurring in the Western Tethys (W Tethys), the Muschelkalk, the Eastern Tethys (E Tethys) and northwestern Panthalassa (NW Panthalassa) during the Early (E. T.) and the Middle Triassic (M. T.), as well as endemic species. The numbers within the circular segments represent the number of species belonging to the corresponding palaeogeographic province.

FIG. 12. Rank-abundance distribution and guild structure of the investigated bivalve fauna. n = total number of individuals.

FIG. 13. Assumed life positions of epibyssate (1–12), cementing (13), free-lying (14–19), endobyssate (20–24), shallow burrowing (25–28) and deep burrowing (29–32) bivalve genera with respect to the substratum. Abbreviations: 1 = *Plagiostoma*; 2 = *Pteria*; 3 = *Mysidioptera*; 4 = *Neomorphotis*; 5 = *Ornithopecten*; 6 = *Chlamys* (*Praechlamys*); 7 = '*Pecten*'; 8 = *Pleuronectites*?; 9 = *Asoella*?; 10 = *Avichlamys*?; 11 = *Amphijanira*?; 12 = Aviculopectinoidea n. gen.; 13 = *Umbrostrea*?; 14 = *Entolium*; 15 = *Praedicerocardium* n. gen.; 16 = *Gervillaria*; 17 = *Leptochondria*; 18 = *Entolioides*; 19 = *Scythentolium*; 20 = *Joannina*; 21 = *Cultriopsis*; 22 = *Pinna*; 23 = *Atrina*; 24 = *Modiolus*; 25 = *Schafhaeutlia*; 26 = *Elegantinia*; 27 = *Heminajas*?; 28 = *Unicardium*; 29 = *Romaniamya* n. gen.; 30 = Anomalodesmata indet. A; 31 = Anomalodesmata indet. C; 32 = Anomalodesmata indet. B; 33 = *Tubiphytes*-microbial buildup.

FIG. 14. Bivalve species richness throughout the Early and Middle Triassic based on data shown in Table 1. The star marks the investigated bivalve fauna. *Abbreviations:* A = Aegean; B = Bithynian; CF = Cassian Formation; D = Dienerian; Fassan = Fassanian; G = Griesbachian; I = Induan; JF = Jena Formation; LM = Leidapo Member; Longobard = Longobardian; MF = Meissner Formation; P = Pachycardientuffe; Pel = Pelsonian; Sm = Smithian; TK = Trochitenkalk Formation; VF = Virgin Formation. Absolute ages according to Cohen *et al.* (2013; updated). Information about the relative duration of substages come from Nawrocki & Szulc (2000), Götz *et al.* (2005), Jattiot *et al.* (2018), Li *et al.* (2018). See text for further information.

FIG. 15. Rarefaction analysis of the reported bivalve fauna from Dobrogea (star) compared with those of other Middle Triassic (M. T.) as well as Early Triassic (E. T.) bivalve faunas. Data used from Stiller (2001), Hofmann *et al.* (2013*a*, *b*, 2014), Foster *et al.* (2015, 2019), Hautmann *et al.* (2015), Foster & Sebe (2017) and Friesenbichler *et al.* (2019).

TABLE CAPTIONS

TABLE 1. Species richness of selected Early and Middle Triassic bivalve faunas. Modified after Friesenbichler *et al.* (2019). Information about the age of the lithological units comes from Fürsich & Wendt (1977), Broglio Loriga *et al.* (1990), Brack & Rieber (1993), Brack *et al.* (1996), Szente & Vörös (2003), Manfrin *et al.* (2005), Stiller & Bucher (2008), Hagdorn & Nitsch (2009), Shigeta *et al.* (2009), Balini *et al.* (2010), Hofmann *et al.* (2013*a*, *b*, 2014, 2015), Popa *et al.* (2014), Urlichs (2014), Hausmann & Nützel (2015), Hautmann *et al.* (2015), Foster *et al.* (2015, 2017), Brayard *et al.* (2017), Foster & Sebe (2017) and Foster *et al.* (2019).

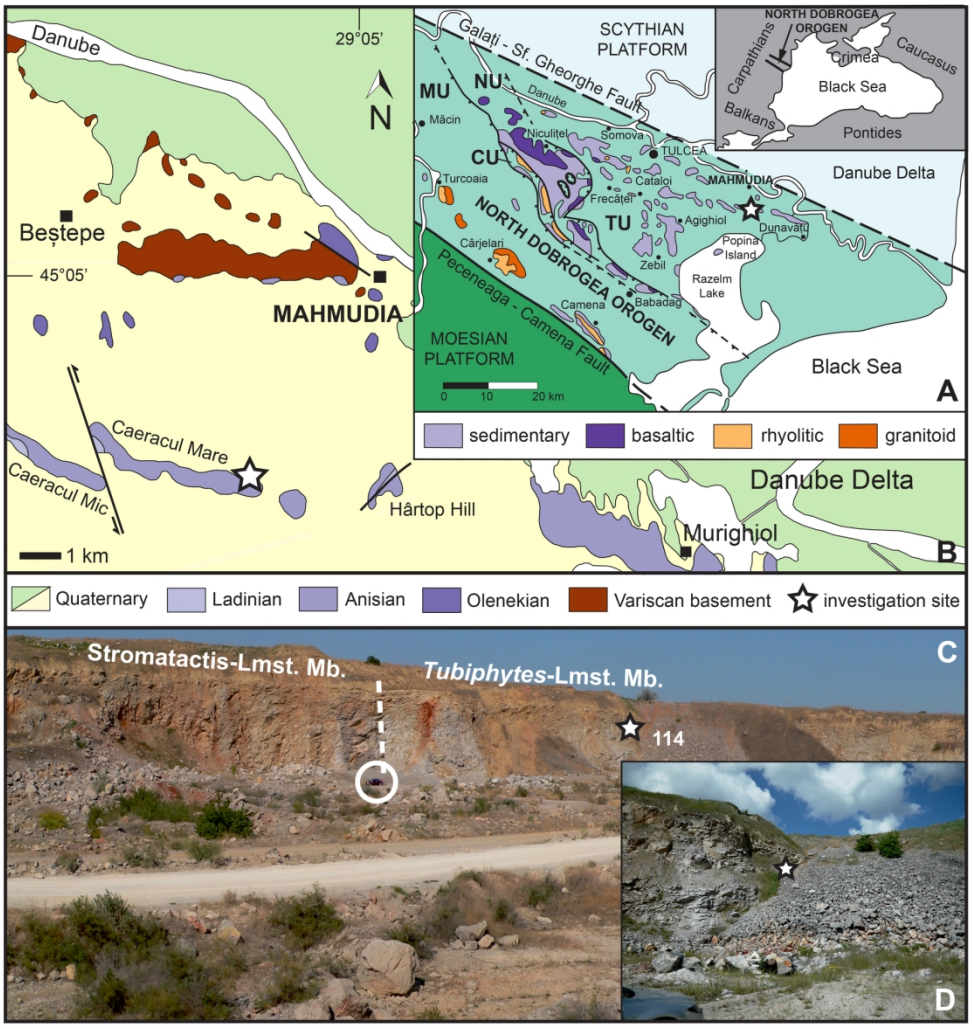


FIG. 1. A, tectonic map of the North Dobrogea Orogen. Inset map showing the regional geological setting and the location of the North Dobrogea Orogen. *Abbreviations*: CU = Consul Unit; MU = Măcin Unit; NU = Niculițel Unit; TU = Tulcea Unit. B, geological map of the Mahmudia region. C, field photograph showing the Bithynian sediments of the Caerace Formation. The dashed line marks the boundary between the Stromatactis-Limestone Member and the overlying *Tubiphytes*-Limestone Member. Car (in circle) for scale. D, close-up view showing the position of the sample site. Modified after Grădinaru (2000), Popa *et al.* (2014), Forel & Grădinaru (2018), Nützel *et al.* (2018) and Grădinaru & Gaetani (2019).

165x171mm (300 x 300 DPI)

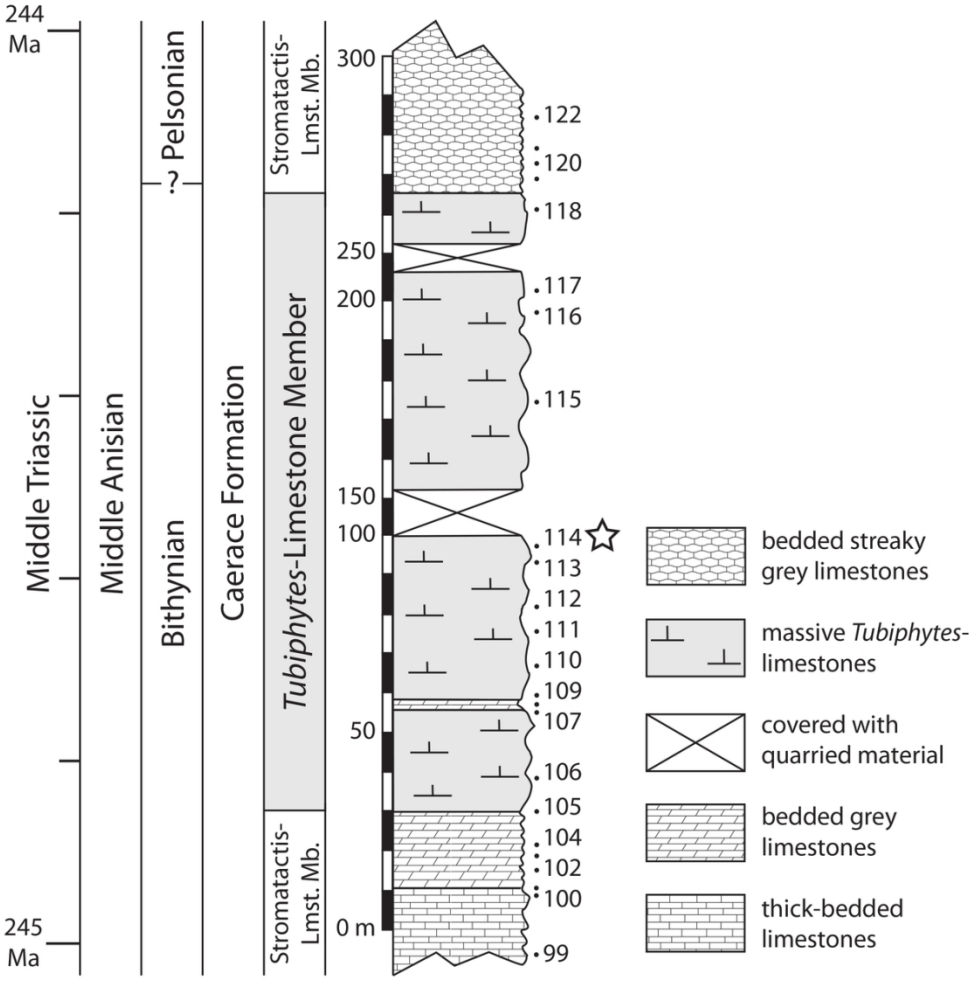


FIG. 2. Stratigraphic column of the Mahmudia Quarry. Numbers 99–122 represent sample levels from previous works (Nützel *et al.* 2018; Grădinaru & Gaetani 2019). The star marks the sample level that yielded the bivalve specimens described herein.

109x108mm (300 x 300 DPI)

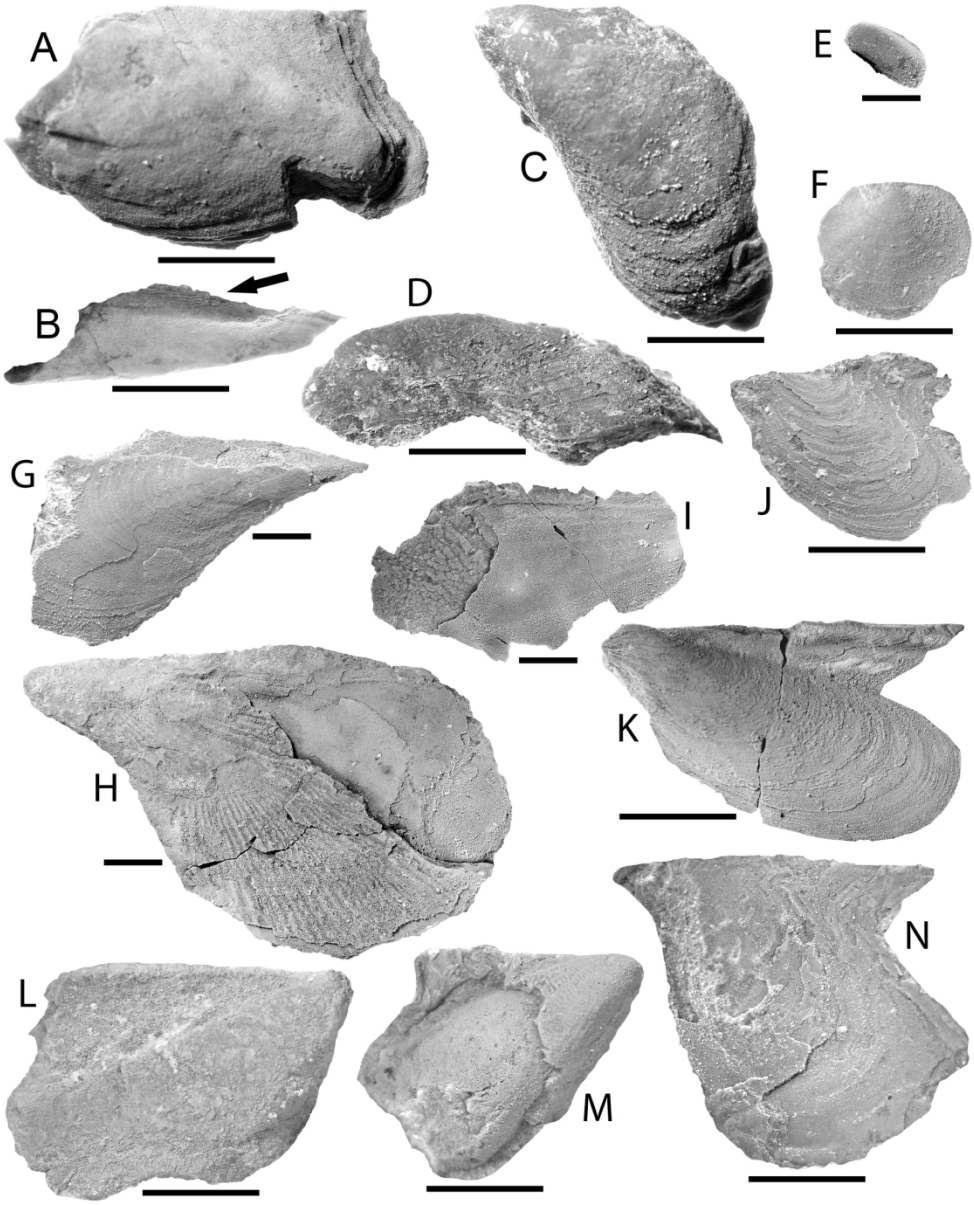


FIG. 3. A–B, *Parallelodon*? sp., LPB IIIL 2001; A, LV; B, dorsal view of A showing the chevron grooves of the duplivincular ligament (arrow). C–D, *Modiolus* sp. A, LPB IIIL 2002; C, LV; D, anterior view of C. E, LV of *Modiolus* sp. B, LPB IIIL 2004. F, RV of *Bositra wengensis* (Wissmann, 1841), LPB IIIL 2008. G, RV of *Pinna simionescui* n. sp., holotype, LPB IIIL 2006. H, LV of *Atrina multicostata* n. sp., holotype, LPB IIIL 2005. I, not oriented valve of *Pinna*? cf. *raibliana* Parona, 1889, LPB IIIL 2007. J–K, LVs of *Pteria sturi* (Bittner, 1895), LPB IIIL 2009 and LPB IIIL 2010. L, RV of *Pteria* sp. A, LPB IIIL 2013. M, RV of *Pteria* sp. B, LPB IIIL 2014. N, RV's interior of *Pteria* cf. *cassiana* (Bittner, 1895), LPB IIIL 2012. Scale bars represent 1 cm (A–D, F–N) and 0.5 cm (E).

165x204mm (300 x 300 DPI)

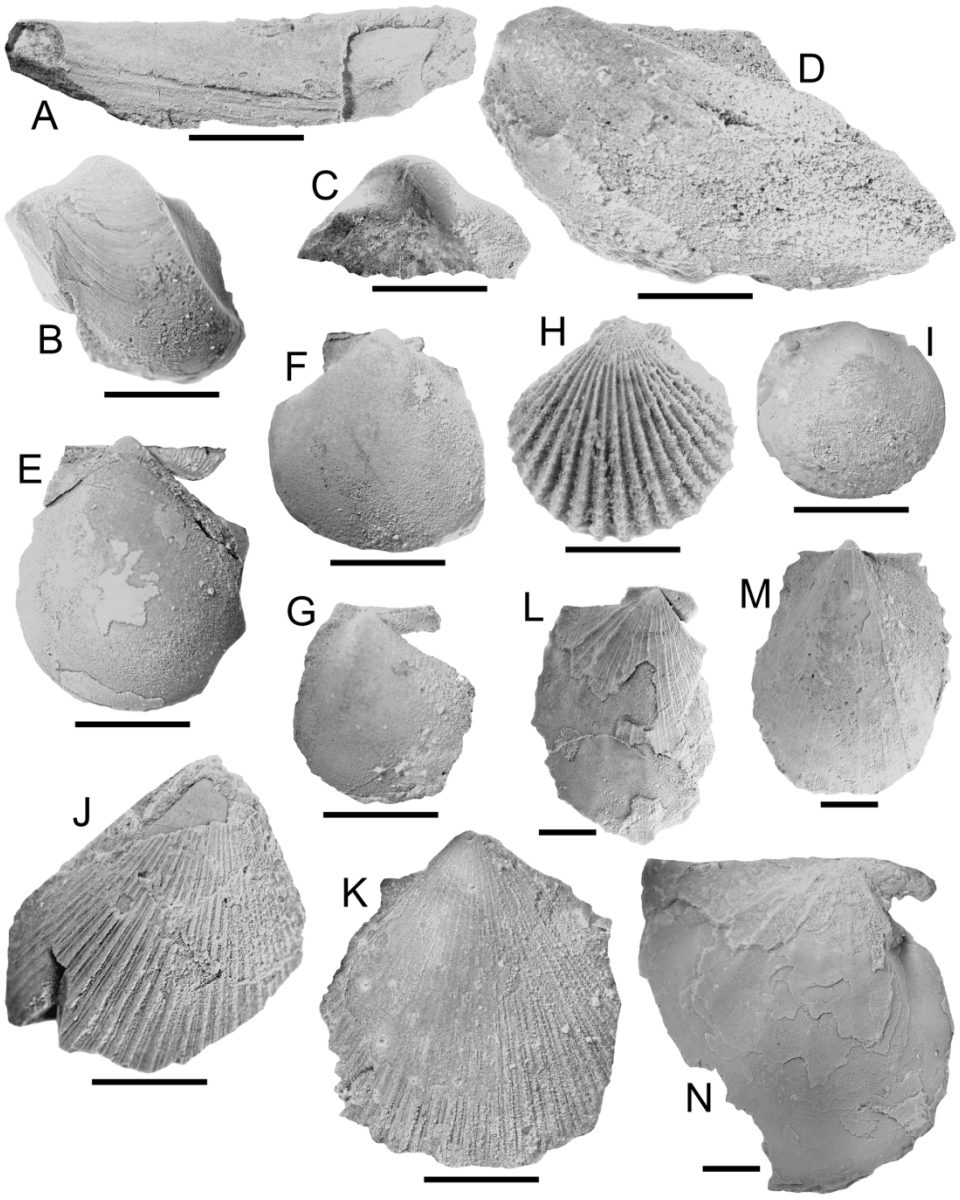


FIG. 4. A, LV of *Cultriopsis* sp., LPB IIIL 2015. B–C, *Gervillaria subelegans* (Chen, 1976), LPB IIIL 2016; B, LV; C, umbonal region of B. D, LV of Bakevelliidae indet., LPB IIIL 2018. E–G, Aviculopectinoidea n. gen. et n. sp.; E, RV, the deep byssal notch and the sculpture of the auricles are well visible, LPB IIIL 2021; F, LV, LPB IIIL 2022; G, RV, LPB IIIL 2023. H, LV of '*Pecten*' *volaris* (Bittner, 1902), LPB IIIL 2019. I, LV of *Asoella*? sp., LPB IIIL 2038. J–K, LVs of *Amphijanira*? aff. *landrana* (Bittner, 1895), LPB IIIL 2024 and LPB IIIL 2025. L–N, *Neomorphotis comta* (Goldfuss, 1833); L and N; RVs, LPB IIIL 2028 and LPB IIIL 2029; M; LV, LPB IIIL 2027. Scale bars represent 1 cm.

165x207mm (300 x 300 DPI)

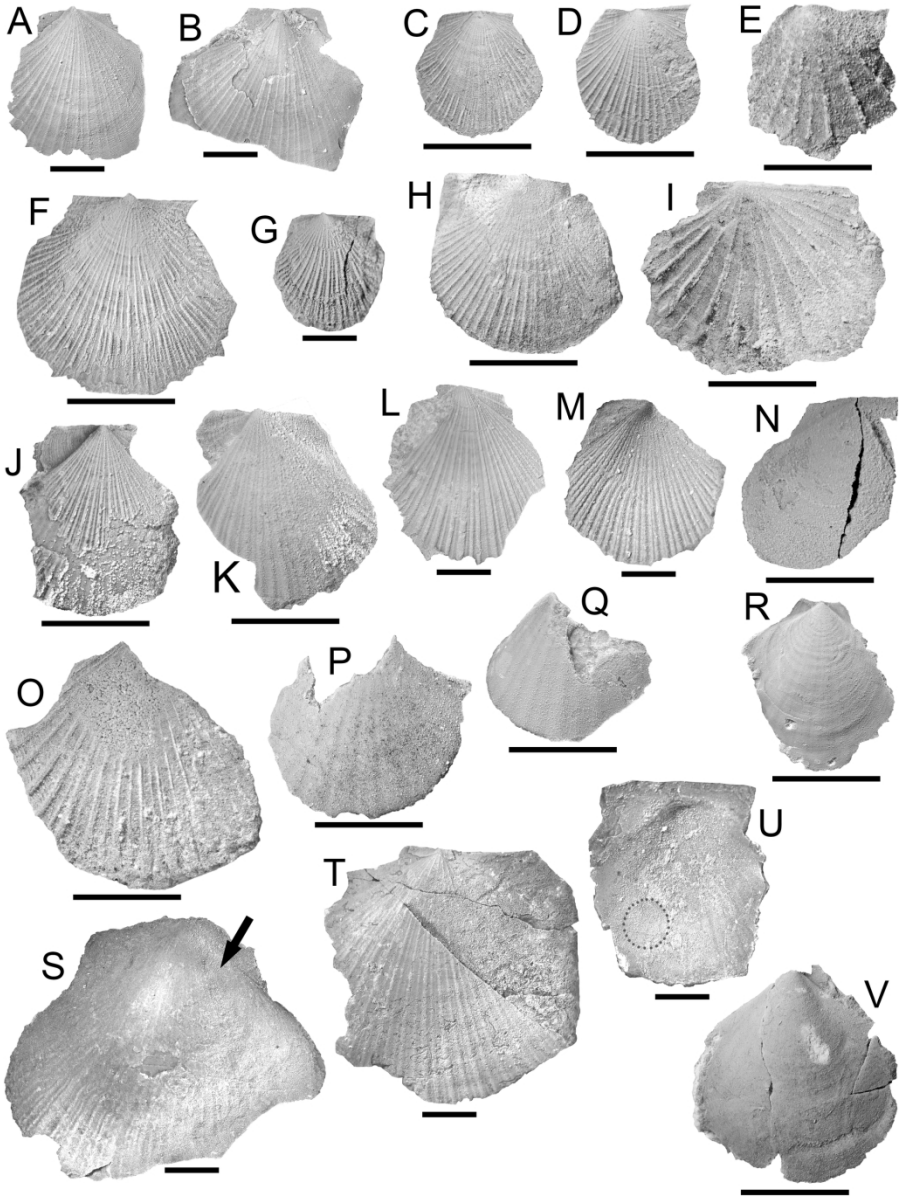
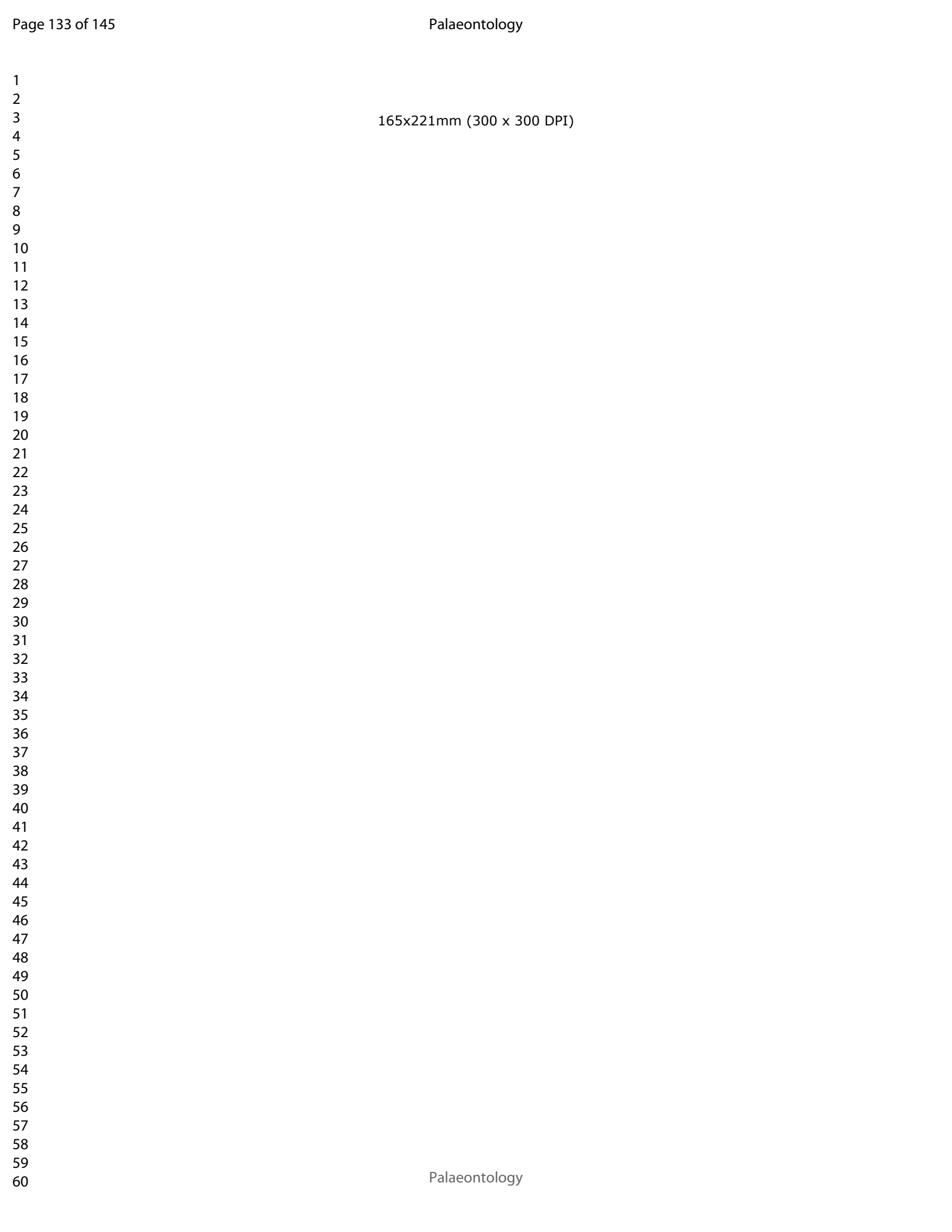


FIG. 5. A–B, LVs of *Leptochondria pervulgata* (Bittner, 1902), LPB IIIL 2039 and LPB IIIL 2040. C–D, LVs of *Leptochondria separata* (Reis, 1926), LPB IIIL 2049 and LPB IIIL 2050. E, LV of *Ornithopecten* cf. *katzeri* (Bittner, 1902), LPB IIIL 2058. F–H LVs of *Leptochondria viezzenensis* (Wilckens, 1909), LPB IIIL 2053, LPB IIIL 2054 and LPB IIIL 2055. I, LV of *Ornithopecten interruptus* (Bittner, 1902), LPB IIIL 2057. J–M, *Chlamys* (*Praechlamys*) *prima* n. sp.; J and L, LVs, the auricle's sculpture is well visible, paratypes, LPB IIIL 2060 and 2061; K, LV, holotype, LPB IIIL 2062; M, external mould of a LV, paratype, LPB IIIL 2063. N, RV of *Pleuronectites*? cf. *balatonicus* (Bittner, 1901), LPB IIIL 2068. O, LV of *Avichlamys*? cf. *nicolensis* (Ogilvie Gordon, 1927), LPB IIIL 2059. P–Q, Pectinidae indet.; P, internal mould of a RV, LPB IIIL 2066; Q, internal mould of a LV, LPB IIIL 2067. R, LV of *Entolium reticulatum* n. sp. showing the shell's reticular sculpture, holotype, LPB IIIL 2070. S–U *Entolioides deeckei* (Parona, 1889). S, LV. Arrow shows the depression subparallel to posterior margin, LPB IIIL 2071. T, LV, LPB IIIL 2072; U, interior of a LV. Dotted line marks the posterior adductor muscle, LPB IIIL 2073. V, LV of *Entolium* sp., LPB IIIL 2159. Scale bars represent 1 cm (A–D, F, H–V) and 0.5 cm (E and G).


165x221mm (300 x 300 DPI)

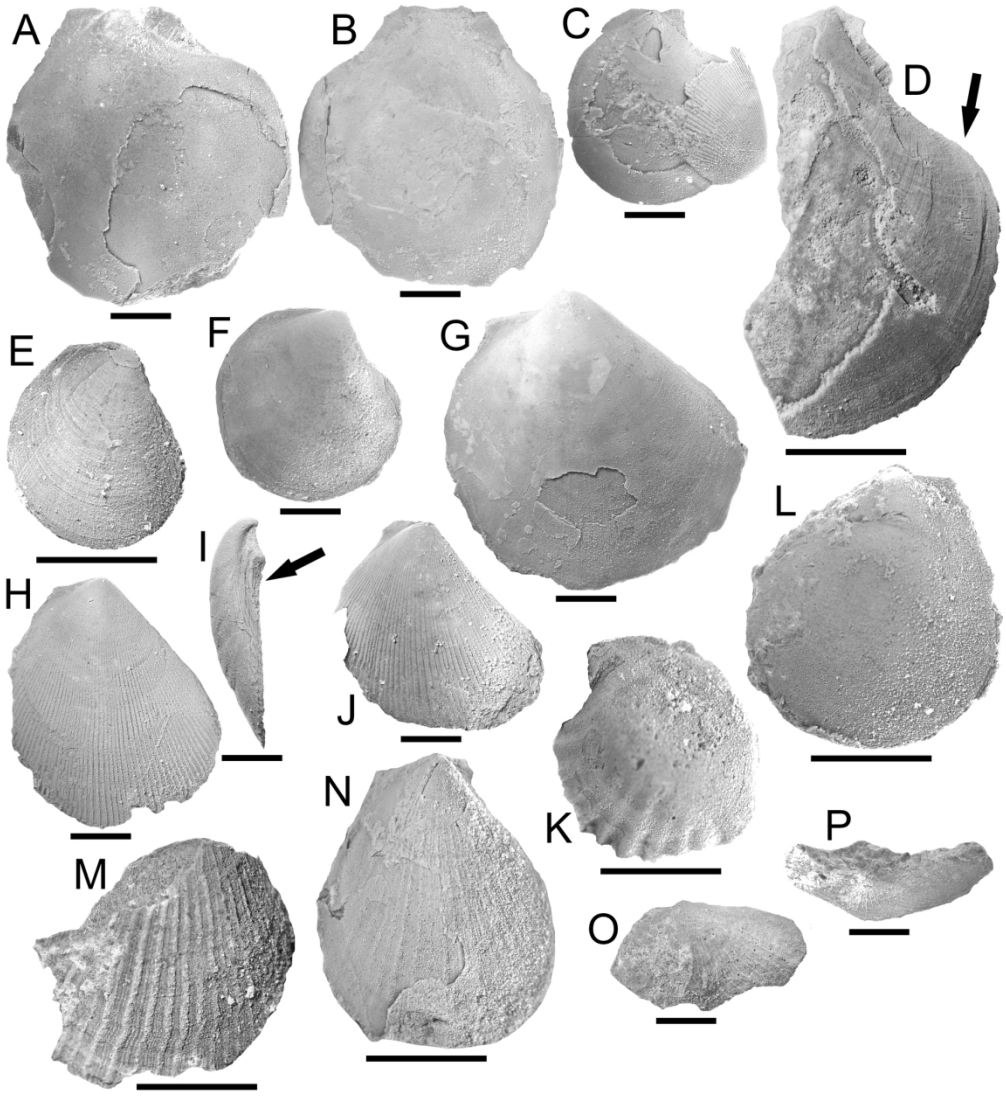


FIG. 6. A–D, *Scythentolium anisicum* n. sp.; A, RV of holotype, LPB IIIL 2075; B, LV of holotype, LPB IIIL 2075; C, RV with *Plagiostoma striatum* (LPB IIIL 2102), paratype, LPB IIIL 2076; D, fragmented RV showing the antimarginal structure (arrow), paratype, LPB IIIL 2082. E–G, RVs of *Mysidioptera fornicata* Bittner, 1895, LPB IIIL 2089, LPB IIIL 2090 and LPB IIIL 2091, the weak radial sculptural elements are best visible in E and G. H–J, *Plagiostoma striatum* (von Schlotheim, 1820); H, RV, LPB IIIL 2102; I, anterior view of a RV showing the lunula (arrow), LPB IIIL 2103; J, RV, LPB IIIL 2104. K, LV of *Umbrostrea*? sp., LPB IIIL 2087. L, LV of an articulated specimen of *Mysidioptera* sp., LPB IIIL 2101. M–N, *Plagiostoma* cf. *angulatum* (Münster, 1841); M, fragmented LV well showing the shell's sculpture, LPB IIIL 2128; N, RV, LPB IIIL 2127. O–P, Monotidae indet., LPB IIIL 2088; O, internal mould of a LV; P, dorsal view of O. Scale bars represent 1 cm.

165x181mm (300 x 300 DPI)

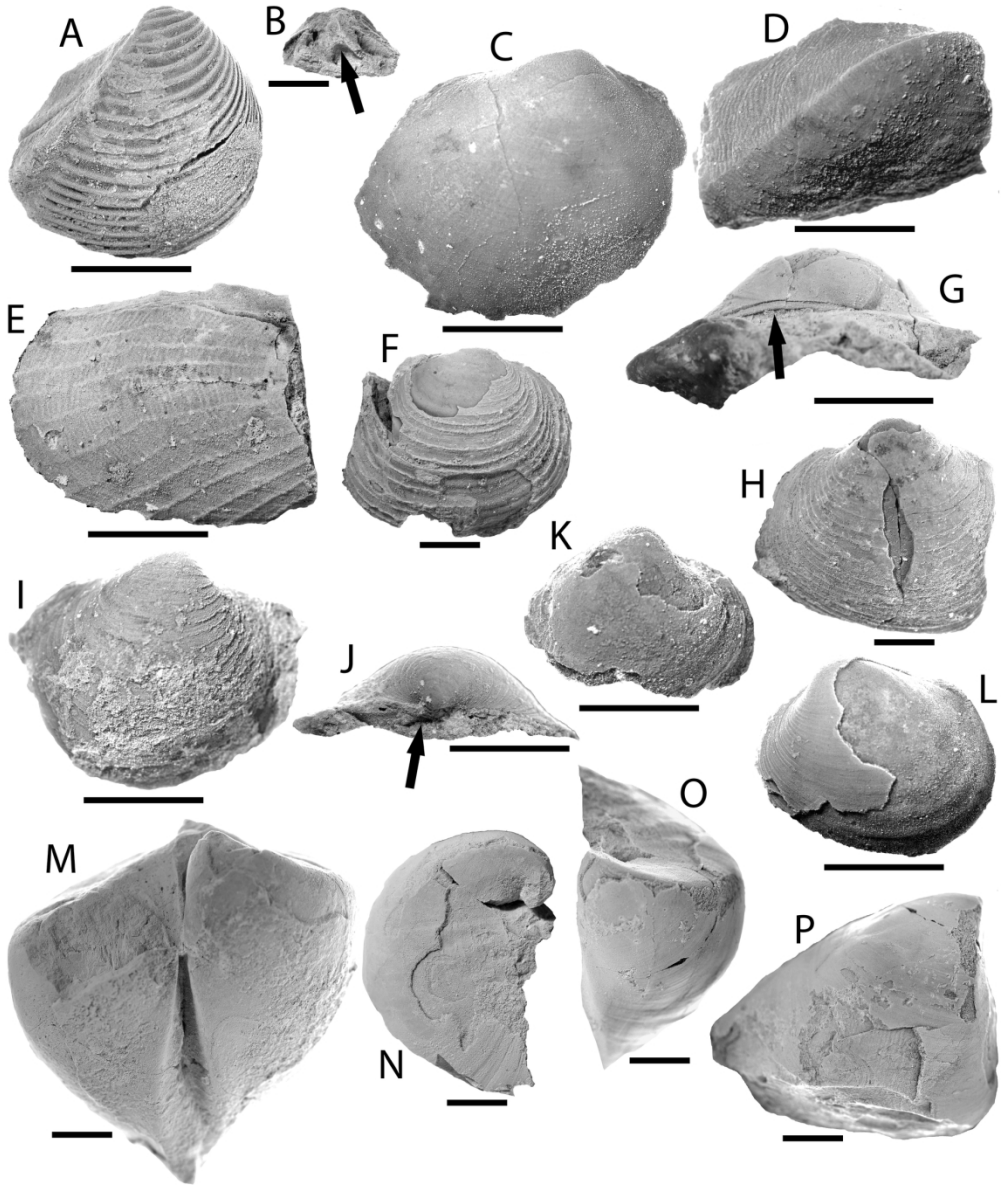


FIG. 7. A–B, *Elegantinia elegans* (Dunker, 1849), LPB IIIL 2130; A, RV's exterior; B, interior of A showing the two merged hinge teeth (arrow). C, RV of *Heminajas*? sp., LPB IIIL 2131. D, RV of *Joannina* aff. *joannae* Waagen, 1906, LPB IIIL 2132. E, fragmented RV of *Myoconcha* sp., LPB IIIL 2133. F–H, *Unicardium schmidii* (Geinitz, 1842); F, RV, LPB IIIL 2134; G, umbonal region of H showing the nymph (arrow); H, LV, LPB IIIL 2135. I–K, *Schafhaeutlia astartiformis* (Münster, 1841); I, RV, LPB IIIL 2137; J, dorsal view of I showing parts of the hinge (arrow); K, RV, LPB IIIL 2138. L, LV of *Schafhaeutlia*? *trigona* (Stoppani, 1858), LPB IIIL 2140. M–P, *Praedicerocardium vetulus* n. gen. et n. sp.; M, dorsal view of an articulated specimen, holotype, LPB IIIL 2142; N, anterior view of a RV, paratype, LPB IIIL 2143; O, dorsal view of N; P, lateral view of N. Scale bars represent 1 cm (A, C–P) and 0.5 cm (B).

165x199mm (300 x 300 DPI)

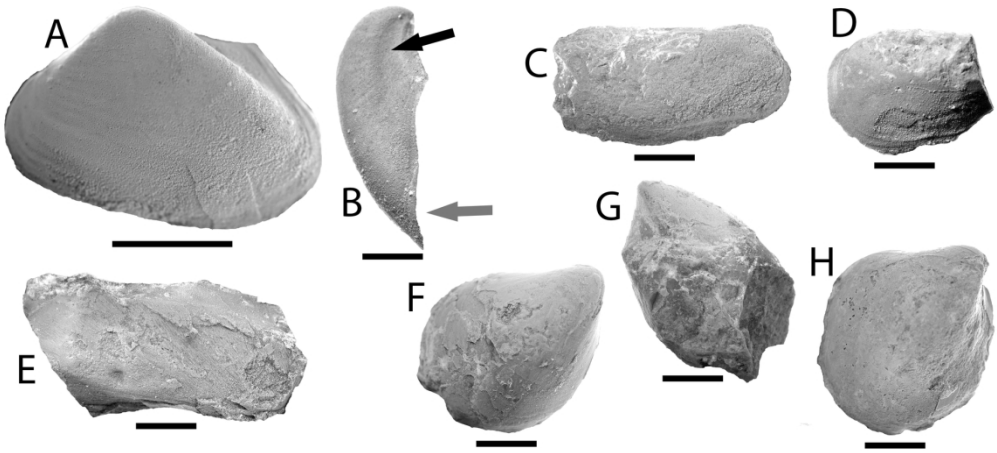


FIG. 8. A–B, *Romaniamya mahmudiaensis* n. gen. et n. sp., holotype, LPB IIIL 2145; A, LV; B, posterior view of A showing the sulcus located dorsally to the umbonal ridge (black arrow) and the shell's narrow gape (grey arrow). C, internal mould of a RV of Anomalodesmata indet. A, LPB IIIL 2148. D, not oriented specimen of Anomalodesmata indet. B, LPB IIIL 2149. E, internal mould of a LV of Anomalodesmata indet. C, LPB IIIL 2147. F–H, *Mytiliconcha* cf. *orobica* Tommasi, 1911; F, RV, LPB IIIL 2155; G, umbonal region of F; H, RV, LPB IIIL 2156. Scale bars represent 1 cm (A, C–H) and 0.5 cm (B).

165x75mm (300 x 300 DPI)

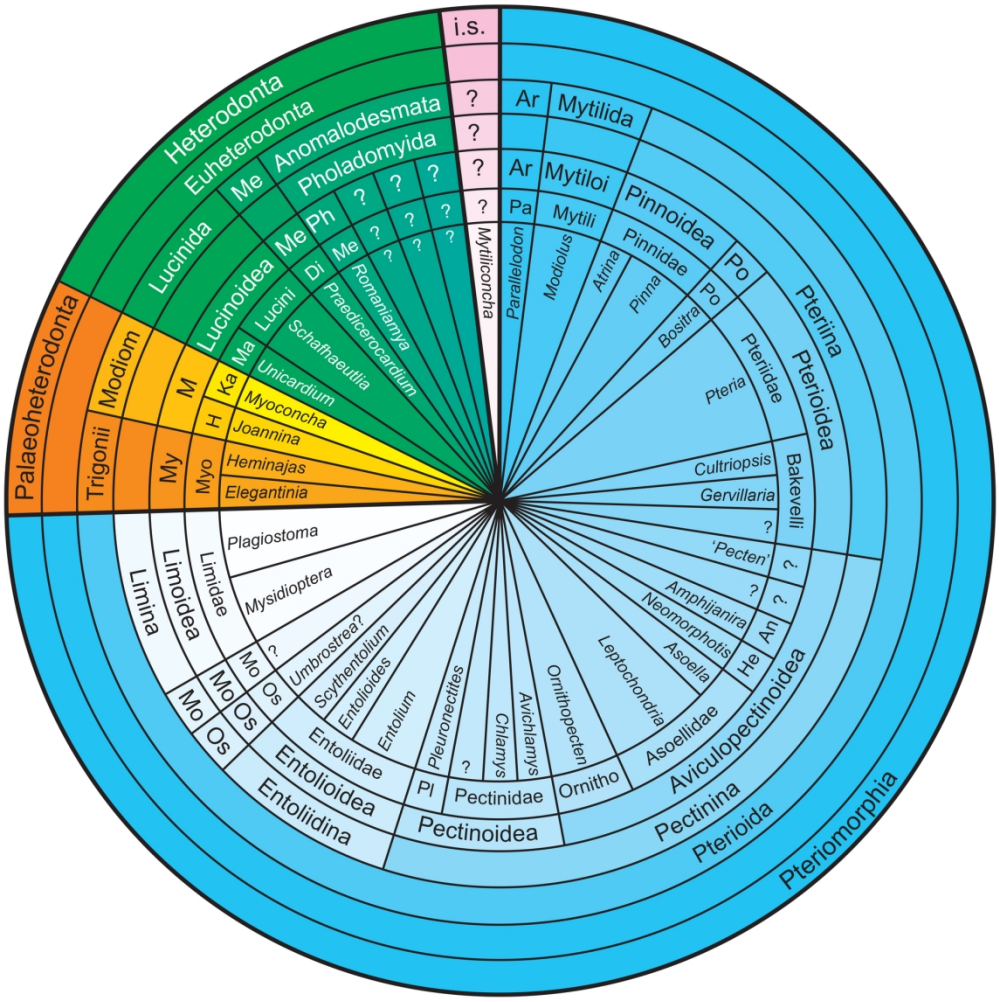


FIG. 9. Pie chart showing the percentage of bivalve genera (innermost circle), families (second innermost circle), superfamilies (third innermost circle), suborders (middle circle), orders (third outermost circle), infraclasses (second outermost circle) and subclasses (outermost circle). *Abbreviations for subclasses*: i.s. = *incertae sedis*. *Abbreviations for orders*: Ar = Arcoida; Me = Megalodontida; Modiom = Modiomorphoida; Trigonii = Trigoniida; ? = uncertain. *Abbreviations for suborders*: Mo = Monotidina; Os = Ostreina; ? = uncertain. *Abbreviations for superfamilies*: Ar = Arcoidea; K = Kalenteroidea; M = Modiomorphoidea; Me = Megalodontoidea; Mo = Monotoidea; My = Myophorioidea; Mytiloi = Mytiloidea; Os = Ostreoidea; Ph = Pholadomyoidea; Po = Posidonioidea; ? = uncertain. *Abbreviations for families*: An = Antijaniridae; Bakevelli = Bakevelliidae; Di = Dicerocardiidae; H = Healeyidae; He = Heteropectinidae; Ka = Kalenteridae; Lucini = Lucinidae; Ma = Mactromyidae; Me = Megadesmidae; Mo = Monotidae; Myo = Myophoriidae; Mytili = Mytilidae; Ornitho = Ornithopectinidae; Os = Ostreidae; Pa = Parallelodontidae; Pl = Pleuronectitidae; Po = Posidoniidae; ? = uncertain. *Abbreviations for genera*: ? = uncertain.

165x166mm (300 x 300 DPI)

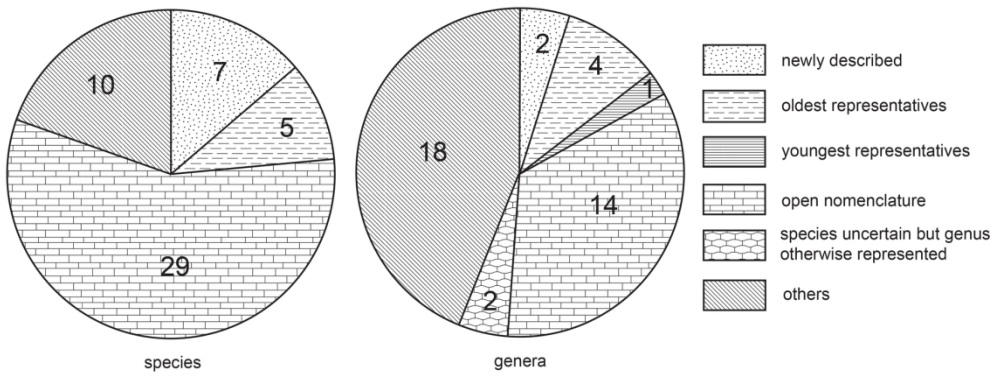


FIG. 10. Pie chart showing the percentage of species (left circle) and genera (right circle) that (i) are newly described, (ii) the oldest and (iii) the youngest occurrence of the taxon, (iv) presented in open nomenclature, (v) species uncertainly belonging to a genus that is confirmed through the presence of another species and (vi) species and genera that do not belong to any of the just mentioned categories. The numbers within the circular segments represent the number of species belonging to the corresponding category.

165x62mm (300 x 300 DPI)

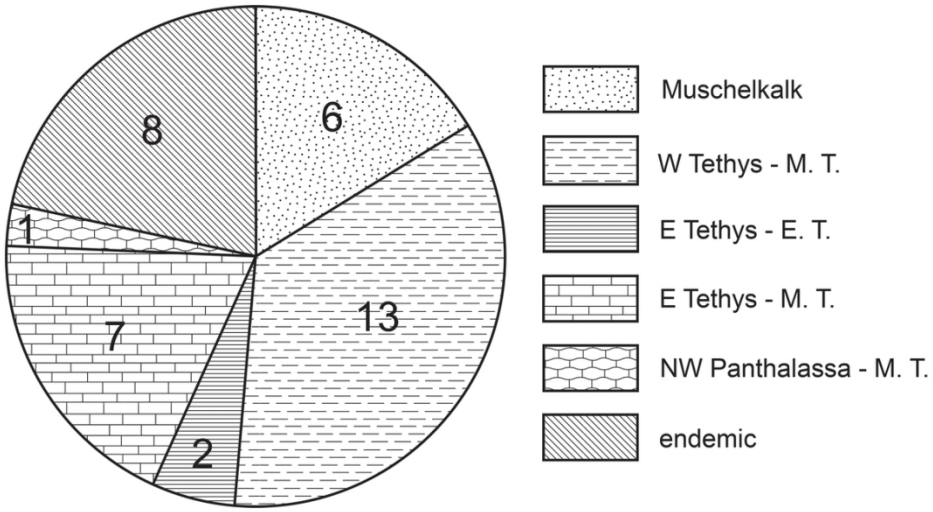


FIG. 11. Pie chart showing the percentage of species occurring in the Western Tethys (W Tethys), the Muschelkalk, the Eastern Tethys (E Tethys) and northwestern Panthalassa (NW Panthalassa) during the Early (E. T.) and the Middle Triassic (M. T.), as well as endemic species. The numbers within the circular segments represent the number of species belonging to the corresponding palaeogeographic province.

109x58mm (300 x 300 DPI)

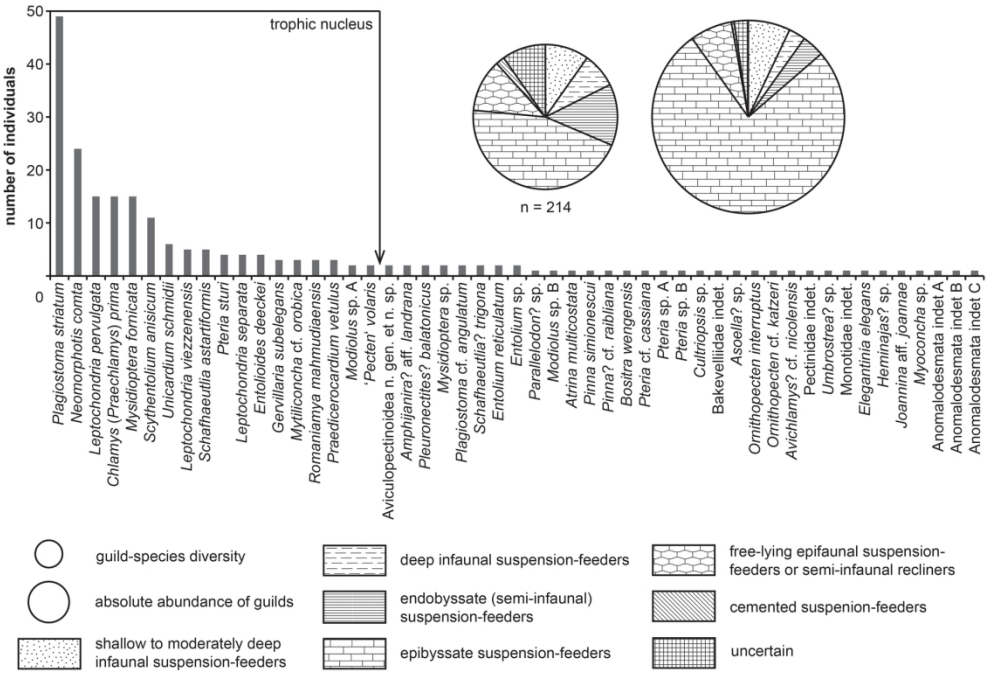


FIG. 12. Rank-abundance distribution and guild structure of the investigated bivalve fauna. n = total number of individuals.

165x112mm (300 x 300 DPI)

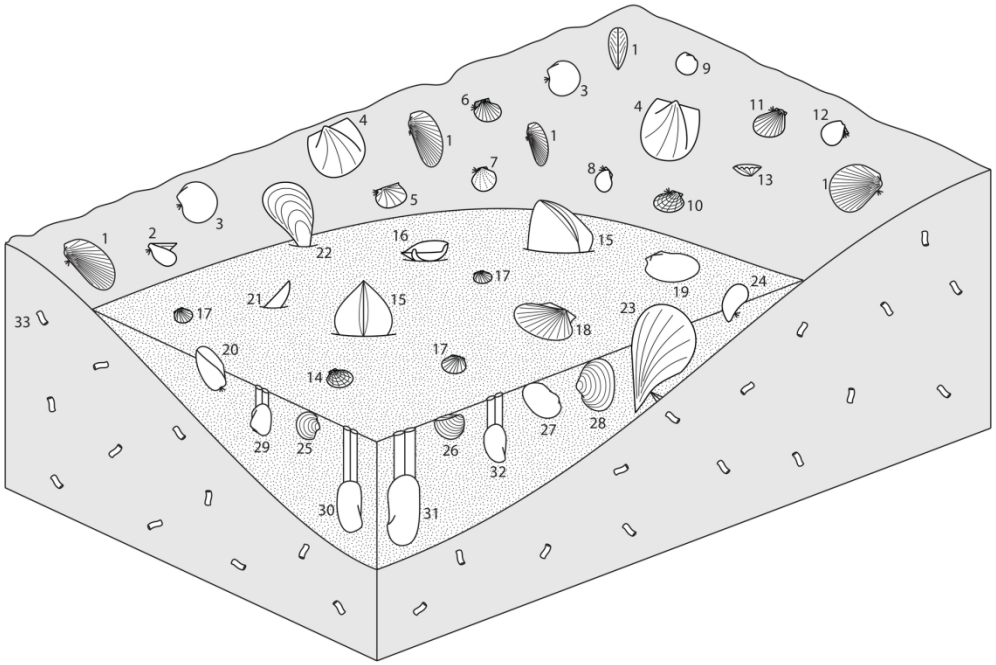


FIG. 13. Assumed life positions of epibyssate (1–12), cementing (13), free-lying (14–19), endobyssate (20–24), shallow burrowing (25–28) and deep burrowing (29–32) bivalve genera with respect to the substratum. Abbreviations: 1 = *Plagiostoma*; 2 = *Pteria*; 3 = *Mysidioptera*; 4 = *Neomorphotis*; 5 = *Ornithopecten*; 6 = *Chlamys* (*Praechlamys*); 7 = '*Pecten*'; 8 = *Pleuronectites*?; 9 = *Asoella*?; 10 = *Avichlamys*?; 11 = *Amphijanira*?; 12 = Aviculopectinoidea n. gen.; 13 = *Umbrostrea*?; 14 = *Entolium*; 15 = *Praedicerocardium* n. gen.; 16 = *Gervillaria*; 17 = *Leptochondria*; 18 = *Entolioides*; 19 = *Scythentolium*; 20 = *Joannina*; 21 = *Cultriopsis*; 22 = *Pinna*; 23 = *Atrina*; 24 = *Modiolus*; 25 = *Schafhaeutlia*; 26 = *Elegantinia*; 27 = *Heminajas*?; 28 = *Unicardium*; 29 = *Romaniamya* n. gen.; 30 = Anomalodesmata indet. A; 31 = Anomalodesmata indet. C; 32 = Anomalodesmata indet. B; 33 = *Tubiphytes*-microbial buildup.

165x111mm (300 x 300 DPI)

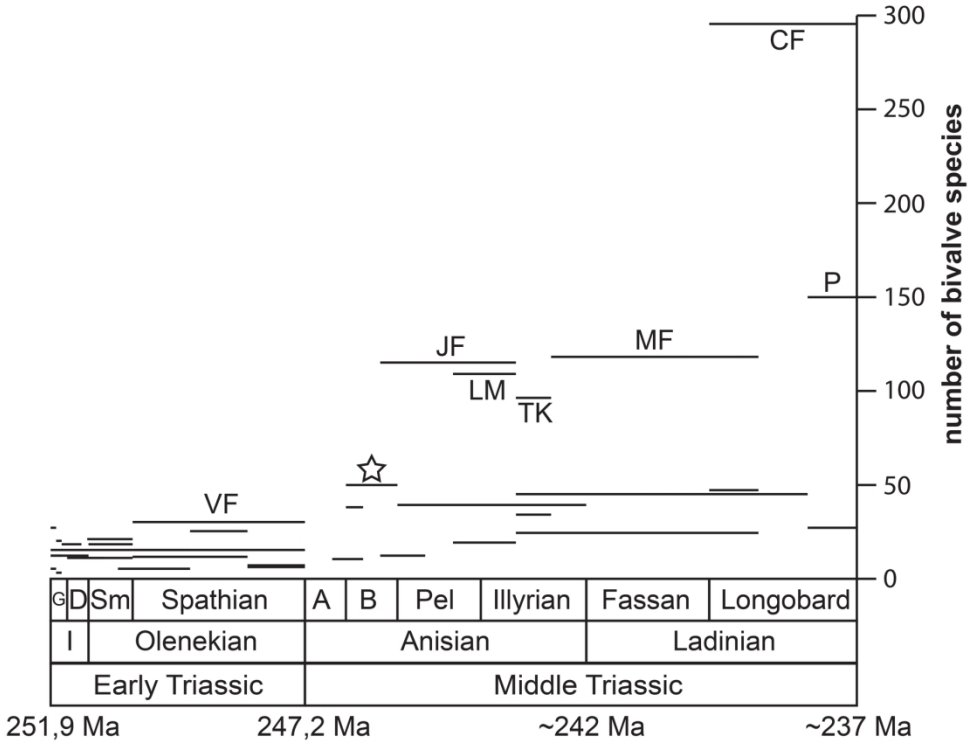


FIG. 14. Bivalve species richness throughout the Early and Middle Triassic based on data shown in Table 1. The star marks the investigated bivalve fauna. *Abbreviations*: A = Aegean; B = Bithynian; CF = Cassian Formation; D = Dienerian; Fassan = Fassanian; G = Griesbachian; I = Induan; JF = Jena Formation; LM = Leidapo Member; Longobard = Longobardian; MF = Meissner Formation; P = Pachycardientuffe; Pel = Pelsonian; Sm = Smithian; TK = Trochitenkalk Formation; VF = Virgin Formation. Absolute ages according to Cohen *et al.* (2013; updated). Information about the relative duration of substages come from Nawrocki & Szulc (2000), Götz *et al.* (2005), Jattiot *et al.* (2018), Li *et al.* (2018). See text for further information.

165x125mm (300 x 300 DPI)

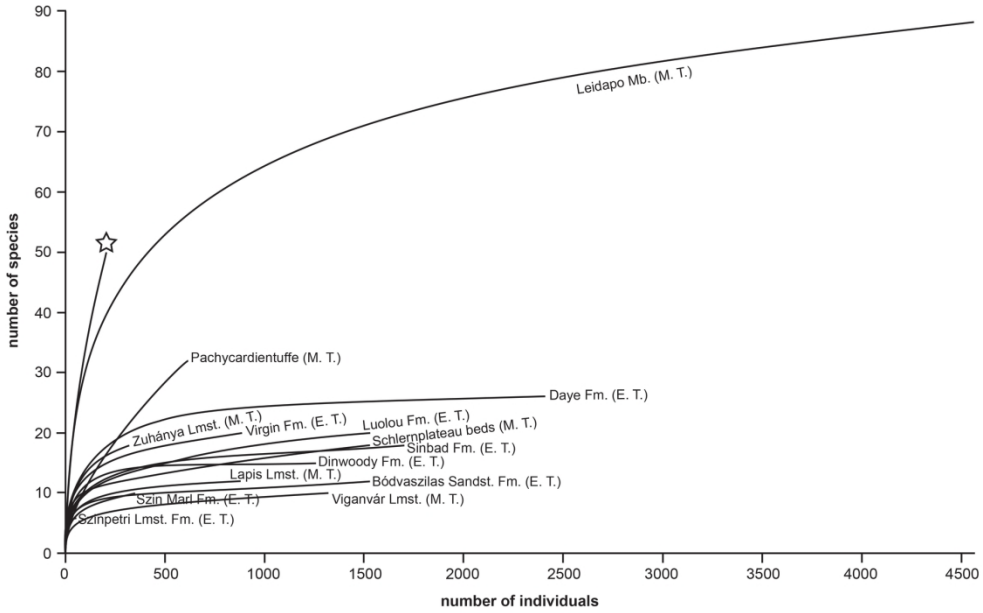


FIG. 15. Rarefaction analysis of the reported bivalve fauna from Dobrogea (star) compared with those of other Middle Triassic (M. T.) as well as Early Triassic (E. T.) bivalve faunas. Data used from Stiller (2001), Hofmann *et al.* (2013*a*, *b*, 2014), Foster *et al.* (2015, 2019), Hautmann *et al.* (2015), Foster & Sebe (2017) and Friesenbichler *et al.* (2018*b*).

165x102mm (300 x 300 DPI)

Lithological Unit	Age	Number of bivalve species	References
Cassian Fm. (Italy)	Longobardian–Julian	296	Laube (1865), Bittner (1895), Pia (1937), Fürsich & Wendt (1977), Zardini (1981), Nützel & Kaim (2014), Hausmann & Nützel (2015)
Schlernplateau beds (Italy)	late Longobardian – early Julian	27	von Wöhrmann & Koken (1892), Friesenbichler *et al.* (2019)
Pachycardientuffe (Wengen Fm., Italy)	late Longobardian	150	Broili (1903), Blaschke (1905), Waagen (1907), Fürsich & Wendt (1977), Friesenbichler *et al.* (2019)
Erfurt Fm. ('Lower Keuper', Germany)	early Longobardian	47	Schmidt (1928, 1938), Urlichs (1982)
Meissner Fm. (upper part of the 'Upper Muschelkalk', Germany)	late Illyrian – early Longobardian	118	Wagner (1897), Schmidt (1928, 1938), Busse (1972), Hagdorn & Mundlos (1982), Hagdorn & Ockert (1993)
Marmolada Limestone (Italy)	middle Illyrian – middle Longobardian	45	Salomon (1895)
Latemar Limestone (Italy)	middle Illyrian – early Longobardian	24	Wilckens (1909)
Trochitenkalk Fm. (basal part of the 'Upper Muschelkalk', Germany)	middle Illyrian	96	Wagner (1897), Schmidt (1928, 1938), Busse (1972), Hagdorn & Ockert (1993), Ockert (1993), Urlichs (1992), Hautmann & Hagdorn (2013)
Karlstadt Fm., Heilbronn Fm., Diemel Fm. ('Middle Muschelkalk', Germany)	early Illyrian – middle Illyrian	34	Schmidt (1928, 1938)
Leidapo Mb. (Quingyan Fm., China)	late Pelsonian – early Illyrian	109	Stiller (2001), Komatsu et al. (2004)
Zuhánya Limestone (Hungary)	late Pelsonian – early Illyrian	19	Foster & Sebe (2017)
Felsőörs Fm. (Hungary)	Pelsonian – Illyrian	39	Szabó *et al.* (1979), Vörös (2003)
Jena Fm. ('Lower Muschelkalk', Germany)	late Bithynian – early Illyrian	115	Wagner (1897), Schmidt (1928, 1938)
Lapis Limestone (Hungary)	late Bithynian – early Pelsonian	12	Foster & Sebe (2017)
Tubiphytes-Limestone Mb. (Romania)	Bithynian	51	this study
Röt Fm. ('Upper Buntsandstein', Germany)	Early Bithynian	38	Wagner (1897), Schmidt (1928, 1938)
Viganvár Limestone (Hungary)	late Aegean – early Bithynian	10	Foster & Sebe (2017)

Csopak Marl (Hungary)	Spathian	15	Broglio Loriga *et al.* (1990), Budai (2008)
Virgin Fm. (USA)	Spathian	30	McGowan *et al.* (2009), Hautmann *et al.* (2013), Hofmann *et al.* (2013*b*)
Szinpetri Limestone Fm. (USA)	late Spathian	6	Foster *et al.* (2015)
San Lucano Mb. (Werfen Fm., Italy)	late Spathian	7	Neri & Posenato (1985), Broglio Loriga *et al.* (1990), Foster *et al.* (2017)
Cencenighe Mb. (Werfen Fm, Italy)	middle Spathian	25	Neri & Posenato (1985), Broglio Loriga *et al.* (1990), Hofmann *et al.* (2015), Foster *et al.* (2017)
Szin Marl Fm. (Hungary)	early – middle Spathian	10	Foster *et al.* (2015)
Val Badia Mb. (Werfen Fm., Italy)	early Spathian	15	Broglio Loriga *et al.* (1990), Hofmann *et al.* (2015), Foster *et al.* (2017)
Lower Shale unit (Thaynes Gr., USA)	late Smithian – early Spathian	5	Brayard *et al.* (2017)
Sinbad Fm. (USA)	Smithian	18	Hofmann *et al.* (2014)
Hidegkút Fm. (Hungary)	Smithian	15	Bittner (1901), Broglio Loriga *et al.* (1990)
Campil Mb. (Werfen Fm., Italy)	Smithian	21	Broglio Loriga *et al.* (1990), Hofmann *et al.* (2015), Foster *et al.* (2017)
Zhitkov Fm. (Russia)	Dienerian – Smithian	11	Shigeta *et al.* (2009)
Gastropod Oolite (Werfen Fm., Italy)	late Dienerian – early Smithian	11	Broglio Loriga *et al.* (1990), Hofmann *et al.* (2015), Foster *et al.* (2017)
Seis Mb. (Werfen Fm., Italy)	Dienerian	18	Broglio Loriga *et al.* (1990), Hofmann *et al.* (2015), Foster *et al.* (2017)
Dinwoody Fm. (USA)	Griesbachian – Dienerian	15	Hofmann *et al.* (2013*a*)
Köveskál Fm., Arács Fm., Alcsútdoboz Fm. (Balaton Highland, Hungary)	Griesbachian – Dienerian	12	Broglio Loriga *et al.* (1990)
Lazurnaya Bay Fm. (Russia)	Griesbachian	12	Shigeta *et al.* (2009)
Bódvaszilas Sandstone Fm. (Hungary)	middle Griesbachian – Smithian	12	Foster *et al.* (2015)
Luolou Fm. (China)	middle Griesbachian	20	Hautmann *et al.* (2015)
Andraz Horizon (Werfen Fm., Italy)	middle Griesbachian	3	Foster *et al.* (2017)
Mazzin Mb. (Werfen Fm., Italy)	early – middle Griesbachian	12	Broglio Loriga *et al.* (1986, 1990), Hofmann *et al.* (2015), Foster *et al.* (2017)
microbialite unit	early Griesbachian	26	Foster *et al.* (2019)

(Daye Fm., China)			
Tesero Oolite (Werfen Fm., Italy)	late Changhsingian – early Griesbachian	5	Broglio Loriga *et al.* (1986, 1990), Foster *et al.* (2017)